LIBRARY
FISH & WILDLIFE SERVICE
PACIFIC OCEANIC FISHERY
INVESTIGATIONS

OCT 23 1952

MINISTRY OF AGRICULTURE AND FISHERIES

FISHERY INVESTIGATIONS

SERIES II VOL. XVIII No. 2

Reproduction of Oysters in the Rivers Crouch and Roach, Essex, during 1947, 1948 and 1949

E. W. KNIGHT-JONES, D. Phil.

Marine Biology Station, University College of North Wales, Bangor
Formerly Senior Scientific Officer on the Staff of the
Ministry of Agriculture and Fisheries

LONDON: HER MAJESTY'S STATIONERY OFFICE

1952

PRICE 3*s.* 6*d.* NET

MINISTRY OF AGRICULTURE AND FISHERIES

FISHERY INVESTIGATIONS
Series II Vol. XVIII No. 2

REPRODUCTION OF OYSTERS IN THE RIVERS CROUCH AND ROACH, ESSEX, during 1947, 1948 and 1949

E. W. KNIGHT-JONES, D. Phil.

Marine Biology Station, University College of North Wales, Bangor.
Formerly Senior Scientific Officer on the Staff of the
Ministry of Agriculture and Fisheries

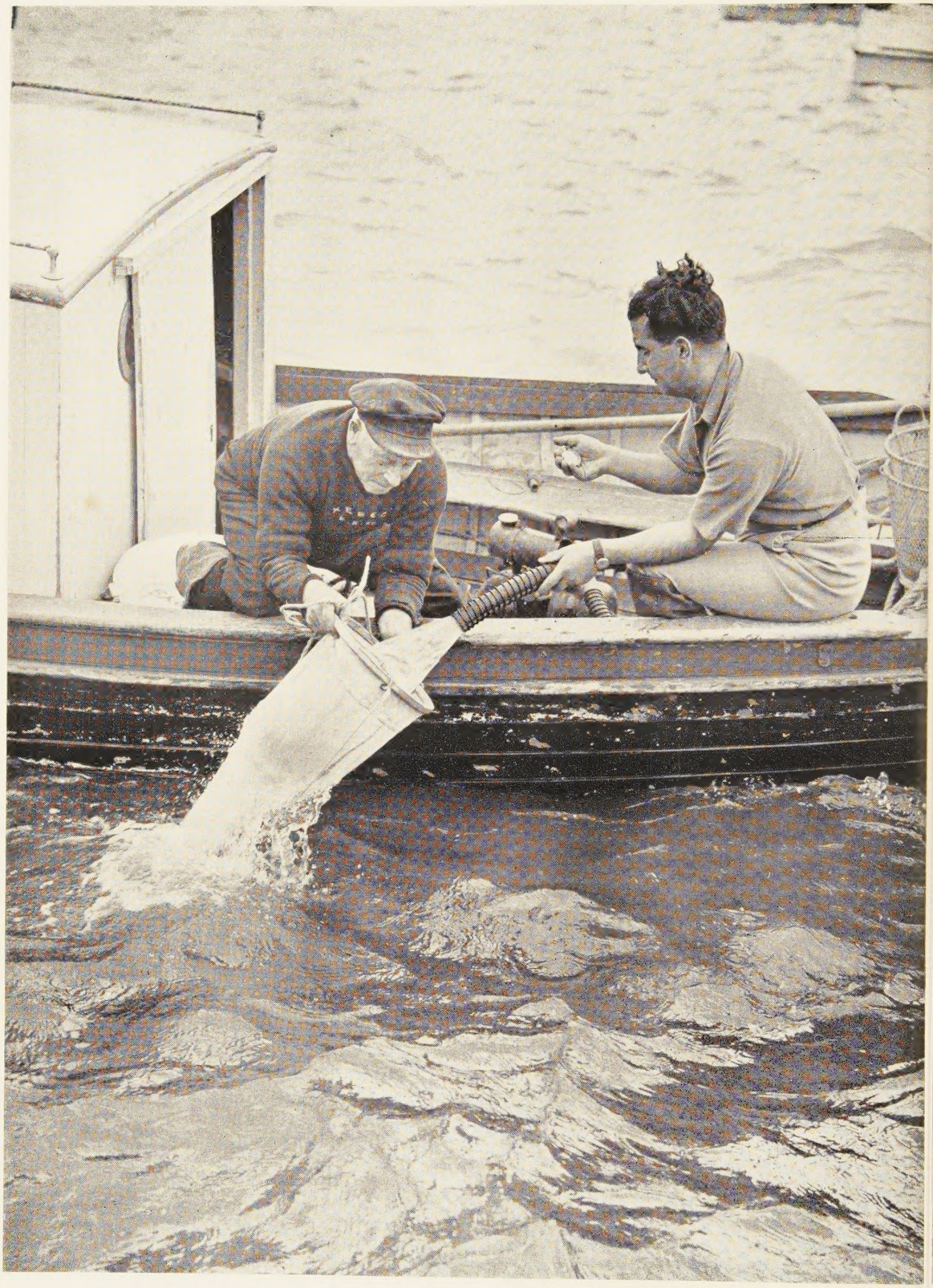
LONDON: HER MAJESTY'S STATIONERY OFFICE
1952

CONTENTS

		Page
I	INTRODUCTION	3
II	GENERAL FEATURES OF THE AREA	3
III	HYDROGRAPHY AND THE WEATHER	4
IV	NANNOPLANKTON ESTIMATIONS	6
V	SAMPLING OF OYSTER LARVAE	10
VI	SPAWNING PERIODICITY	11
VII	LIBERATION OF LARVAE DURING TIDAL CYCLE	14
VIII	SIZE, GROWTH AND SURVIVAL OF LARVAE	16
IX	DISTRIBUTION OF BREEDING STOCKS AND OF LARVAE	24
X	INTENSITY AND DISTRIBUTION OF SPATFALL	25
XI	SETTING OF THE BARNACLE, ELMINIUS MODESTUS	30
XII	SETTING OF OTHER SESSILE ORGANISMS COMPETING WITH OYSTER SPAT	32
XIII	USE OF ARTIFICIAL COLLECTORS FOR SPAT	35
XIV	LOSSES AMONGST SETTLED SPAT	37
XV	SUMMARY OF EVENTS DURING THE THREE SEASONS	38
XVI	A DISCUSSION OF THE FACTORS AFFECTING SPAT PRODUCTION	44
	SUMMARY	45
	ACKNOWLEDGMENTS	46
	REFERENCES	47

Digitized by the Internet Archive
in 2025

https://archive.org/details/fishery-investigations-series-ii_1952_18_2



[*Graphic Photo Union*

Mr. M. N. Mistakidis pumping a 100 l. plankton sample from the R. Crouch near Burnham, assisted by Mr. Gurton, from a launch which is moving slowly forward through the water. The intake hose, drawing water from a depth of 1 metre, cannot be seen, being further towards the bow.

Reproduction of Oysters in the Rivers Crouch and Roach, Essex, during 1947, 1948 and 1949

By E. W. KNIGHT-JONES, D.Phil.
*Shellfish Research Station, Burnham-on-Crouch**

I. INTRODUCTION

NE of the aims of the recently established Shellfish Research Station at Burnham-on-Crouch to investigate the conditions necessary for the revival of the Essex oyster industry, which is w considerably less flourishing than formerly. Several factors contributed to its decline. om 1914 to 1918 wide areas, which were formerly productive, were neglected and became othered with mud and pests. The American slipper-limpet, *Crepidula fornicata*, which is now erwhelmingly abundant on most grounds, is said to have increased enormously during this riod. Post-war revival was retarded by the heavy mortality of 1920 (Orton, 1924), which nsiderably reduced oyster stocks and caused men to leave the industry for other work. ccessive spatfall failures followed. Orton (1937) wrote " The failure of the spatfall in the t summer of 1933 shook faith in the resiliency of English oysters, but the fine spatfall in 1935 the Thames Estuary has restored both the beds and the faith ". The millions of young oysters rived from this spatfall were practically wiped out, just before they came to market, in the ere winter of 1939–40 (Cole, 1940). The equally severe weather early in 1947 was accompanied a similar very heavy mortality. When research began at Burnham in 1947 oyster stocks re said to be smaller than at any time within living memory.

The fecundity of the oyster gives the best hope of revival. It is probable that every individual er a year old spawns during each season, producing from 40,000 to 2,000,000 eggs and that ortality is negligible during the initial period of incubation (Cole, 1941) but very heavy during e subsequent planktonic stage. Korringa (1941) estimated that generally, in the Oosterschelde, less than 10 per cent of the planktonic larvae survive to the settlement stage. Evidently great increase in oyster production might confidently be expected if the death rate amongst vae could be reduced.

Studies by Orton (1936), and regular opening of incubating oysters by oystermen, had indicated awning to be satisfactory in Essex, but the planktonic stage had not been studied. Part of the st-war oyster research programme (Cole, 1951) was to apply to Essex creeks routine plankton mpling, as used in oyster-breeding experiments at Conway (Cole, 1936; 1939), and at the same ne to study the environmental conditions likely to affect growth and survival. The records the first three years' work on this enquiry into the planktonic stage form the basis of this count.

II. GENERAL FEATURES OF THE AREA

The size and arrangement of the Rivers Crouch and Roach and their tributary creeks are dicated in Fig. 1. They are essentially sea-water drainage channels in land which was once al. Today they are kept within narrow bounds by sea-walls. Their depth at low water is r the most part less than 8 metres, reaching a maximum of 15 metres about half a mile below e confluence of the Roach and Crouch. Parts of the channel in the lower Crouch are sandy, t generally the bottom is of soft mud, hardened in places by shells or outcrops of clay. The st oyster grounds, which are covered with muddy shells, lie at various depths and occur from e mouth of the Crouch to distances of about a mile above Fambridge and Paglesham in the ouch and Roach respectively. Most of the grounds lie in shallow water and in the headwaters, pecially in the Paglesham area. Those worked from the Fisheries Laboratory are shown with eir names in Fig. 1. In addition to the Fisheries motor smack, two large commercial oyster edgers are based at Burnham, each of which works about six hand-dredges. A few smaller ats work in the Paglesham area and from Althorne Creek.

* Now at Marine Biology Station, University College of North Wales, Bangor.

15471 A 2

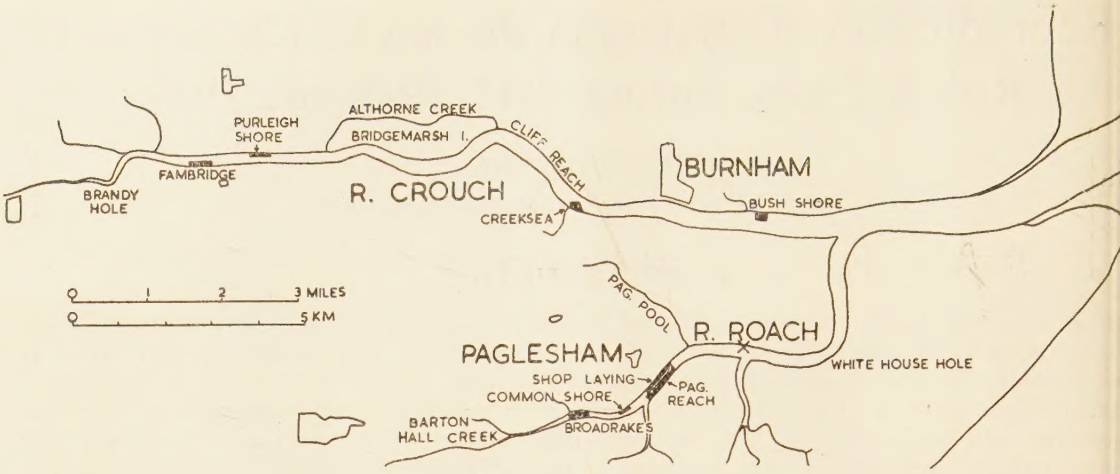


FIG. 1

Map of Rivers Crouch and Roach. Oyster grounds which are worked from the Shellfish Research Static Burnham-on-Crouch, are shown as black areas. The position of the test slate referred to as "Roa Mud" (Fig. 8) is marked X.

The fauna has been investigated by Mistakidis (1952), who found it rather similar to that the Oosterschelde, the great oyster-producing basin of Holland, judging from the records Hoek and his associates (1884). The slipper-limpet, *Crepidula fornicata*, is now overwhelming abundant, as on many Dutch beds today. Mr. P. R. Walne, who is investigating the biology this pest in Essex, finds that very large areas are covered with *Crepidula* at a density of ov 1,000 per square metre. It forms the bulk of the benthic biomass. Fixed algae are very spar for stable substrata are scarce. The plankton in neighbouring waters has been studied by We (1938).

III. HYDROGRAPHY AND THE WEATHER

Ditches from the neighbouring land drain through the sea-walls at many points, and a sm stream, the Crouch, flows over a weir about five miles above Fambridge, but the area drain is small, the rainfall is low and the quantity of fresh water introduced is negligible in normal yea In summer there are usually no haliclines and no residual seawards drift of the water. Af heavy winter rains, the salinity at Fambridge did not fall much below 30°/₀₀ at low water and ev then the water which returned with the flood tide was more than 33°/₀₀. Summer rains w absorbed immediately by the dry, flat ground. After very heavy rain during the night 28th–29th Ju 1947, a series of samples was taken from a depth of ½ a metre at H.W. along the length Paglesham Pool, a shallow creek about 25 metres wide and 2·5 kilometres long (Fig. 1). T salinities at the upper end, middle and mouth were respectively 35·5°/₀₀, 36·0°/₀₀ and 36·2° Evaporation often caused salinity in the head waters to be higher than in the sea outside. exceeded 37°/₀₀ during low water at Fambridge, after the hot, dry summer of 1949 (Fig. *Ophiura texturata* was numerous above Fambridge, a witness to the fully-saline conditions the

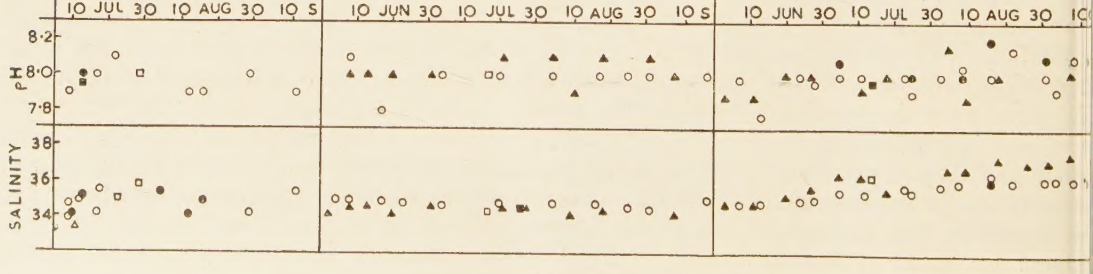


FIG. 2

Records of pH and salinity. The position and state of tide of each sample are indicated as follows Burnham, H.W. ○; L.W. ●; Fambridge, H.W. △; L.W. ▲; Paglesham, H.W. □; L.W. ■.

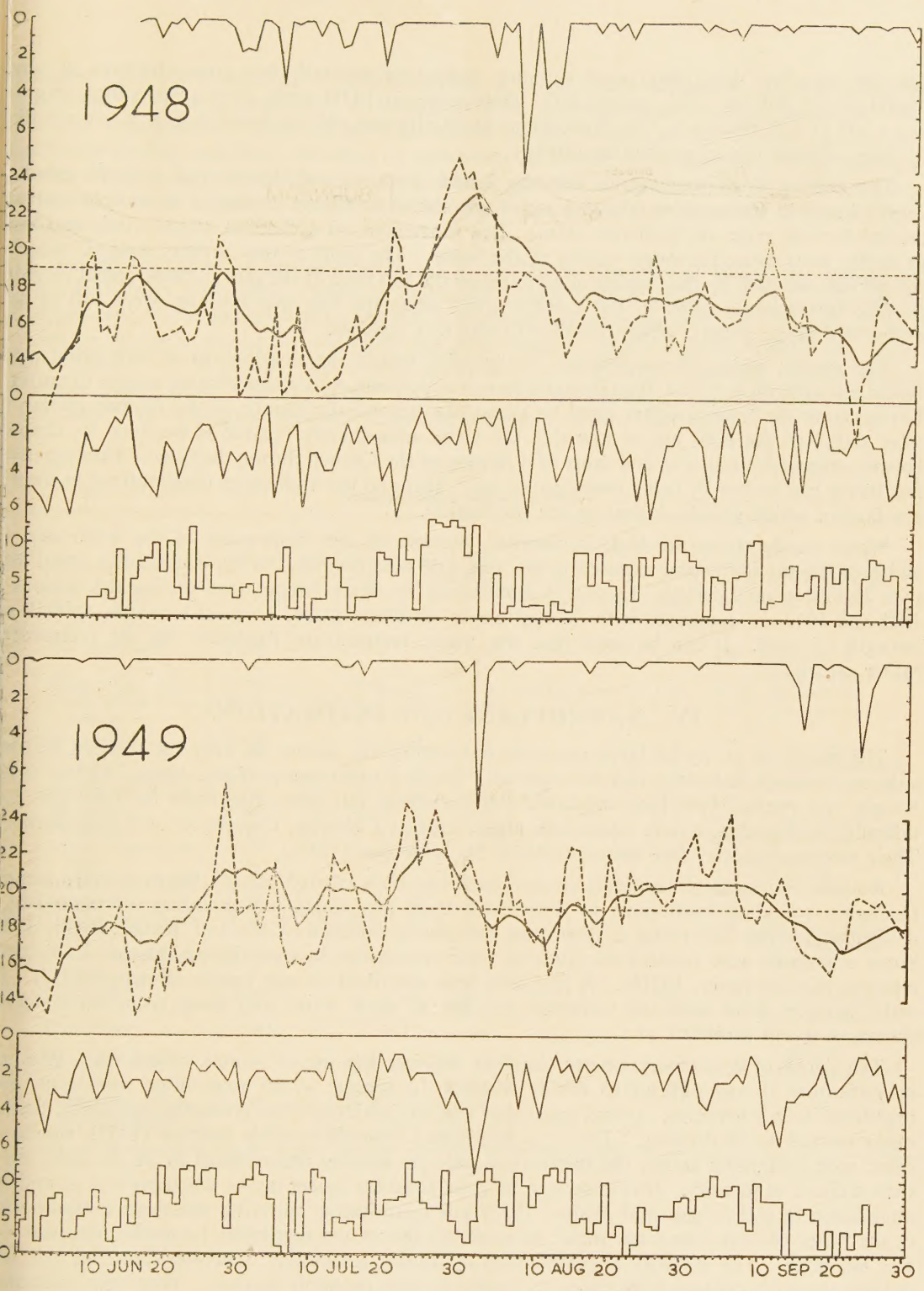


FIG. 3

cords of weather conditions and water temperature during 1948 and 1949. The water temperature ctuations (continuous lines) are similar to those of the air temperature (dotted lines), but slighter. dotted line is ruled at 19°, for good growth of oyster larvae occurred only when the water temperature proached or exceeded this level (but see p. 44). The wind is given as Beaufort numbers, which are the ans of twice-daily observations at Southend-on-Sea, carried out by Mr. E. J. Cotgrove, F.R.Met.S., l kindly made available by the Piermaster, Captain J. C. Johnson, F.R.G.S., R.N.R. The scale of sunshine n hours, that of rainfall in inches. The wind and rainfall scales are inverted, because the cloudiness turbidity associated with increases in these variables probably have an unfavourable effect on growth oyster larvae, i.e. an opposite effect from that of increased sunshine or temperature. High rates of wth and survival of larvae occurred only at the end of July, 1948, when unusually prolonged sunshine and calm weather led to a rapid rise in temperature to the highest level recorded.

The pH was low throughout each summer, indicating generally low concentrations of phyto plankton. It did not often exceed 8·0. Only once, at 12.00 noon after a hot sunny morning was a pH of 8·2 observed. The fluctuations in salinity and pH, indicated in Fig. 2, are not likely to have affected oyster production directly.

The vertical tidal range varies between 3 and 5 metres and tidal currents attain speeds o 2 or 3 knots at spring tides (about 1 metre per second). Floats immersed in mid-channel wer carried for five miles on moderate tides. This movement, in a channel which winds and varie in depth, must cause thorough mixing of the water. The swirl of the currents, helped, except i the calmest weather, by the lapping of wavelets on the soft mud of the shores, causes great turbidity Surface townettings, taken in the lower Crouch when the tide was running, were full of san grains and faecal pellets, which resembled those of *Crepidula*.

The simple, piston-like movement of the tides makes the distribution of swimming oyst larvae less difficult to follow than it would be in a wide basin with a complicated system of current Larvae from the lower reaches must be swept out beyond the mouth of the Crouch during th later stages of the ebb, but at low tide the water immediately outside is confined to channe between exposed sandbanks and most of it returns to the Crouch during the flood. Comparative few larvae can be lost by being swept out to sea. This and the high water temperatures in summ are factors which greatly favour oyster production.

Water temperatures are high in summer, because of the shallowness of the water and th width of the muddy shores exposed to the sun, and also because the sea outside is a shoal are with extensive sand banks. In Fig. 3 fluctuations in water temperature during the seasons 1948 and 1949 are compared with fluctuations in air temperature, hours of sunshine, rainfall an strength of wind. It can be seen that the water temperature followed the air temperatu rather closely.

IV. NANNOPLANKTON ESTIMATIONS

The mouth of an oyster larva measures only about 10μ across, so only the smallest diatom such as *Navicula halophila*, can be ingested. Feeding experiments (Cole, 1936; 1939; Bru Knight and Parke, 1940) have indicated that the larvae rely upon flagellates for food and ha difficulty in digesting minute non-motile algae, such as *Chlorella*, *Coccomyxa* and *Synechococc* Their filtering capacity has been calculated by Jørgensen (1943).

Routine estimates of nannoplankton abundance were carried out by filtering water samp through a collodion membrane, to concentrate them fifty times, and counting the organisms a haemacytometer following a procedure previously outlined (Cole and Knight-Jones, 194 Some organisms were isolated for study of their systematics by quantitative dilution into cult medium (Knight-Jones, 1951*b*). A few have been described as new species (Butcher, 1952). T water samples were collected whenever possible at slack water and away from wave-expo shores, to avoid turbidity.

The depth of a haemacytometer chamber requires the use of 4 mm. objectives. With magnification it was difficult to decide whether 1μ specks, which were often numerous, w organisms or silt particles. It was concluded that the majority were probably organisms, beca many seemed to be dividing. The 1·5μ flagellate *Chromulina pusilla* Butcher (1952), which often seen swimming across the microscope field, is quickly immobilised in bright light an then difficult to identify. It is known to be good food for oyster larvae when present in suffic abundance (Knight-Jones and Walne, 1951) but quantitative culturing indicated concentrati in sea water of only 3 or 4 per mm.^{3}, so probably few of the numerous 1μ specks observed w this flagellate. The majority appeared pale in colour, resembling *Synechococcus*, but this f did not appear in cultures from Essex, so the specks were probably bacteria. They were particul numerous in turbid samples. Experiments at Conway by Mr. P. R. Walne have shown no gro of oyster larvae with bacteria as food: Imai and Sato (1949) have also obtained evidence bacteria are of little direct value as food to microplankton animals, so fluctuations in abund of these 1μ specks are of doubtful importance.

It was also difficult to distinguish between immobilised chrysomonads and Chlorellac Large (5–10μ) species of *Chlorella* could be recognised by their distinct cell wall and green col but culturing showed that species of *Nannochloris*, only 2μ in size and yellowish-green like n

flagellates, were often abundant. Before making a count the haemacytometer was examined briefly under a 16 mm. objective. If flagellates were common, several could be seen moving within the wide field of view. Even *Chromulina pusilla* (1–2μ) can be detected at this low magnification whilst moving. Absence of movement in all the organisms seen in the field was taken as evidence that they were non-motile forms, probably Chlorellaceae. If some were seen moving, then other similar organisms which were motionless were counted as immobilised flagellates.

A preliminary survey of the nannoplankton in the Rivers Crouch and Roach was carried out on 12th–13th July, 1947, after a week of dull, cold, rough weather (Table 1). The composition and abundance of the nannoplankton varied considerably from place to place. Flagellates were very sparse, except in the upper reaches of the River Roach. When a similar survey was undertaken at the end of the month, after two weeks of fine, warm weather, flagellates were somewhat less sparse, being about 5–10 per mm.^{3} Oyster larvae were then showing considerable growth, so this density of flagellates must be considered adequate as food for them.

TABLE 1

Nannoplankton Surveys, 1947

Date	Place	Tide	pH	Temp. °C.	1μ specks	Diatoms	Other non-motile forms	Flagellates		Total >1μ	Organisms identified
								>10μ	2–10μ		
July 12	Burnham, a.m. ...	H.W.	—	—	7	0·25	0·75	—	1·0	2·0	*Nitzschia* *Rhizosolenia*
	Fambridge, p.m.	H.W.	7·9	16·0	29	0·5	0·25	—	1·5	2·25	*Rhizosolenia*
	1 mile above Fambridge.	H.W.	7·9	16·5	20	0·5	—	—	0·5	1·0	*Rhizosolenia*
13	Roach Mouth ...	½ ebb	7·9	17·0	102	1·5	—	—	1·0	2·5	*N. closterium* *Navicula halophila*
	White House Hole	½ ebb	—	17·0	96	—	2·0	0·5	4·5	7·0	Gymnodiniaceae
	Paglesham Reach	¾ ebb	8·0	17·0	66	—	1·0	—	6·0	7·0	—
	Broadrakes ...	¾ ebb	7·9	18·0	40	0·5	—	—	9·5	10·0	chrysomonads
	Burnham... ...	L.W.	8·0	18·0	30	3·5	—	0·5	3·0	7·0	Gymnodiniaceae
28	Upper Paglesham Pool.	H.W.	—	—	47	0·5	—	—	4·5	5·0	*Rhizosolenia* *Nitzschia*
	Paglesham Reach	H.W.	—	—	71	1·5	—	—	4·5	6·0	—
	Roach Mouth ...	½ ebb	—	—	50	0·5	—	—	2·5	3·0	—
29	Upper Paglesham Pool.	H.W.	7·9	23·4	38·5	0·5	—	0·5	3·5	4·5	12μ cryptomonad 12μ *Platymonas*
	Lower Paglesham Pool.	H.W.	8·0	23·2	51	1·0	1·5	—	6·5	9·0	*Nitzschia*
31	Cliff Reach ...	½ flood	—	—	28	0·33	—	—	4·0	4·33	5μ chrysomonad 10μ *Platymonas*
	Fambridge ...	½ flood	—	—	117	—	—	—	14·5	14·5	Perhaps some were *Chlorella*
	Burnham... ...	H.W.	—	22·3	63	—	—	—	10·0	10·0	Active flagellates
Aug. 1	Tollesbury Fleet, R. Blackwater.	L.W.	—	21·8	12·5	2·0	—	—	5·5	7·5	Small *Nitzschia*

Periodical sampling throughout the summer of 1947 showed flagellates always present a densities varying between 0·5 and 17 per mm.^{3} (Table 2). Diatoms were common during Jul and early August but were absent from the samples during the remainder of August. The weathe was remarkably sunny during late July and the whole of August, producing uniformly high wate temperatures (Fig. 11). Probably production of flagellates kept supplies of nutrient salts lo during this period, which may have accounted for the scarcity of diatoms.

TABLE 2

Nannoplankton Sampling, 1947, R. Roach

Date	Place	Tide	pH	Temp. °C.	1μ specks	Diatoms	Other non-motile forms	Flagellates >10μ	Flagellates 2–10μ	Total >1μ	Organisms identified
July 13	Paglesham Reach	¾ ebb	8·0	17	66	—	1·0	—	6·0	7·0	—
23	Paglesham Reach	½ ebb	—	—	59·5	—	—	—	1·5	1·5	*Chromulina pusilla*
28	Paglesham Reach	H.W.	—	—	71	1·5	—	—	4·5	6·0	—
29	Lower Paglesham Pool.	H.W.	8·0	22·4	51	1·0	1·5	—	6·5	9·0	Biraphideae
Aug. 2	White House Hole	L.W.	—	—	32	—	—	—	3·0	3·0	—
7	Paglesham Reach	½ ebb	—	—	57	1·0	9·0	—	2·0	12·0	—
12	Paglesham Reach	½ ebb	—	—	28	—	—	—	2·0	2·0	—
18	Paglesham Reach	L.W.	—	—	61	—	—	—	4·0	4·0	—
28	Paglesham Reach	H.W.	—	—	41·5	—	—	—	17·5	17·5	—
Sept. 4	White House Hole	L.W.	—	—	146	—	—	—	7·0	7·0	—
11	Paglesham Reach	H.W.	—	—	67	—	0·5	—	5·0	5·5	—

Nannoplankton Sampling, 1947, Lower Crouch

July 12	Burnham... ...	H.W.	—	—	7	0·25	0·75	—	1·0	2·0	*Nitzschia* *Rhizosolenia*
13	Burnham... ...	L.W.	8·0	18	30	3·5	—	0·5	3·0	7·0	15μ Gymnodiniac
17	Burnham... ...	H.W.	8·0	19	25	1·5	—	—	1·5	3·0	*Navicula*
	Burnham... ...	L.W.	—	—	48·5	—	—	—	0·5	0·5	Cyanophyceae appeared comm
18	Burnham... ...	H.W.	—	—	79·5	0·5	—	—	4·0	4·5	Biraphideae
	Cliff Reach ...	½ flood	—	—	45·5	1·5	—	—	2·0	3·5	*Nitzschia*
22	Burnham... ...	½ flood	—	19·5	75	1·0	—	—	6·5	7·5	*Chromulina pusill*
31	Cliff Reach ...	½ flood	—	—	28	0·33	—	—	4·0	4·33	5μ chrysomonad 10μ *Platymonas*
	Burnham... ...	H.W.	—	21·9	63	—	—	—	10·0	10·0	Many motile
Aug. 4	Burnham... ...	L.W.	—	21·3	28	—	—	—	4·0	4·0	—
5	Burnham... ...	H.W.	—	20·9	17	—	—	—	3·5	3·5	—
8	Burnham... ...	H.W.	—	21·1	134	0·5	—	—	6·5	7·0	Biraphideae
12	Burnham... ...	L.W.	7·9	21·9	36	0·5	—	—	4·0	4·5	—
13	Crouch Mouth ...	H.W.	—	—	30·5	—	—	—	3·0	3·0	—
16	Burnham... ...	L.W.	7·9	21·5	80	—	—	—	3·5	3·5	—
17	Burnham... ...	H.W.	—	21·8	81	—	—	—	5·5	5·5	—

Nannoplankton Sampling, 1947, Upper Crouch

July 12	Fambridge ...	H.W.	7·9	16·0	29	0·5	0·25	—	1·5	2·25	*Rhizosolenia*
18	Bridgemarsh ...	½ flood	—	—	77	1·0	—	—	3·5	4·5	*Chromulina pusi* Biraphideae
31	Fambridge ...	½ flood	—	—	117	—	—	—	14·5	14·5	Perhaps some *Chlorella*
Aug. 6	Cliff Reach ...	L.W.	—	—	56	0·5	—	—	5·5	6·0	Biraphideae
11	Fambridge ...	½ ebb	—	—	96	—	—	—	3·5	3·5	—
20	Fambridge ...	L.W.	—	—	227	—	—	—	3·0	3·0	—
29	Fambridge ...	H.W.	—	—	110	—	—	—	7·5	7·5	—

The summer of 1948 was in general dull and windy, with short periods of fine weather (Fig. 3). The nannoplankton contained few diatoms, but many other non-motile forms, with *Chlorellaceae* dominant and chain-forming green and brown algae frequently present. Flagellates were usually about 5 per mm.^{3} during the periods of fine weather, but very sparse during bad weather (Table 3). Good growth of oyster larvae occurred during the fine periods.

TABLE 3

Nannoplankton Sampling, 1948, Lower Crouch and Roach

Date	Place	Tide	pH	1μ specks	Diatoms	Other non-motile forms	Flagellates >10μ	Flagellates 2–10μ	Total >1μ	Organisms identified
June										
9	Burnham	H.W.	8·1	77	—	8·0	—	7·0	15·0	*Nitzschia*
24	Burnham	H.W.	—	22	0·5	5·0	—	7·0	12·5	15μ *Coscinodiscus*
July										
4	Burnham	H.W.	8·0	104	—	3·0	3·0	4·5	10·5	15μ cryptomonad
17	Paglesham	H.W.	8·0	31	—	4·0	—	0·5	4·5	—
20	Burnham	H.W.	8·0	28	0·5	0·5	—	0·5	1·5	*Nitzschia* *Platymonas*
26	Paglesham	L.W.	—	37·5	7·0	7·0	0·5	7·5	22·0	—
28	Roach Mouth ...	½ flood	—	43	—	3·0	—	4·0	7·0	—
Aug.										
4	Burnham	H.W.	8·0	83	—	12·0	—	4·0	16·0	10μ chlamydomonad
10	Burnham	H.W.	—	45	—	2·5	—	0·5	3·0	—
17	Burnham	H.W.	8·0	116	—	7·5	—	—	7·5	—
25	Burnham	H.W.	8·0	36·5	—	4·5	—	1·5	6·0	—
31	Burnham	H.W.	8·0	27·5	0·5	7·5	—	0·5	8·5	*Chromulina pusilla*
Sept.										
16	Burnham	H.W.	8·0	29	—	6·0	—	0·5	6·5	—
21	Burnham	H.W.	—	51·5	—	18·0	—	2·0	20·0	—
28	Burnham	H.W.	—	56·5	—	8·5	—	—	8·5	*Rhizosolenia*
	Nannoplankton Sampling, 1948, Upper Crouch									
June										
20	Fambridge	L.W.	8·0	19	—	19·5	—	4·5	24·0	—
28	Fambridge	L.W.	8·0	45	—	5·0	—	1·0	6·0	—
Aug.										
4	Fambridge	L.W.	8·1	20·5	—	5·0	—	7·0	12·0	10μ chlamydomonad
10	Fambridge	L.W.	7·9	43	—	8·0	—	1·5	9·5	—
18	Fambridge	L.W.	8·1	33	—	1·5	—	5·5	7·0	*Chromulina pusilla*
25	Fambridge	L.W.	—	52·5	1·0	9·0	—	1·0	11·0	*Nitzschia* *Euglena*
31	Fambridge	L.W.	8·1	19	—	5·5	0·5	4·0	10·0	*Rhizosolenia* *Euglena* Centrales
Sept.										
7	Fambridge	L.W.	8·0	10·5	0·5	3·0	—	3·0	6·5	*Euglena*
20	Fambridge	L.W.	—	56	2·0	9·0	—	2·0	13·0	*Rhizosolenia*
28	Fambridge	—	—	Numerous much silt	—	7·0	0·5	1·0	8·5	*Euglena*

In 1949 samples were taken from opposite Burnham every few days, one set at high water, another at low water. There was no consistent difference between the two sets (Table 4). The weather was generally sunny, with light breezes. The nannoplankton was varied and somewhat more abundant than in either of the two preceding years, but flagellates were very sparse in late June and early July. Good growth of oyster larvae took place in the River Roach during late June, but unfortunately no nannoplankton samples were taken from the Roach. Sampling was confined to Burnham, where the samples could be examined immediately, to avoid damage to flagellates during transport in hot weather. This arrangement should have been modified when it was seen that the first mass liberations of larvae were confined to the Roach. Larvae were very scarce in the Crouch until September, when good growth occurred with flagellates about 6 per mm.^{3}

Throughout the three seasons the minimum density of organisms greater than 1μ was about 1 per mm.,^{3} the maximum about 50 per mm.^{3} Usually the density lay between 5 and 20 per mm.^{3} This seems a rather slight range of variation. Probably the grazing of animals prevents the nannoplankton of Essex creeks from becoming very abundant. Filter-feeding *Crepidula* carpet vast

areas, whilst plankton animals are so numerous in summer that densities of several oyster larva per litre constitute quite a small part of the total. Rotifers and ciliates, which are abundan probably increase rapidly if flagellates increase, and soon graze them down again. The uniform low pH reflects the sparseness of the nannoplankton.

TABLE 4

Nannoplankton Sampling, 1949, Burnham at High Water

Date	pH	1μ specks	Yeasts	Diatoms	Other non-motile forms	Flagellates		Total >1μ	Organisms identified
						>10μ	2–10μ		
June									
24	8·0	26·25	—	0·25	3·5	—	1·0	4·75	*Nitzschia*
28	8·0	69·5	2	0·25	3·25	—	2·5	8·0	—
July									
5	8·0	104	—	0·3	4·3	—	1·0	5·6	*Rhizosolenia* *Chromulina pusilla*
12	8·0	56	—	0·5	3·0	—	1·5	5·0	—
20	8·0	100·5	—	0·5	6·0	—	7·5	14·0	Centrales
25	7·9	65	0·5	0·5	5·5	—	5·0	11·5	*Platymonas*
Aug.									
2	8·0	102	—	4·0	11·5	—	5·5	21·0	—
8	8·05	58	—	3·0	21·0	0·5	1·5	26·0	—
16	8·05	54·5	—	4·5	6·0	—	11·0	21·5	*Nitzschia*
22	8·15	59·5	—	1·0	10·0	—	2·0	13·0	*Nitzschia*
31	8·0	83·5	—	1·0	8·5	—	2·0	11·5	*Nitzschia*
Sept.									
8	8·1	71	—	—	13·0	—	5·5	18·5	—
18	7·95	69·5	—	—	13·5	—	1·5	15·0	—
22	7·95	57	—	—	14·0	—	1·5	15·5	—

Nannoplankton Sampling, 1949, Burnham at Low Water

June									
24	8·0	99	—	—	2·7	—	0·7	3·4	chrysomonad cryptomonad
29	8·0	89	0·3	0·3	4·0	—	1·3	5·9	—
July									
5	8·1	86	—	0·3	1·3	—	2·6	4·2	*Platymonas*
11	8·9	196	—	0·3	3·7	—	1·7	5·7	*Chromulina pusilla*
25	8·0	219·5	—	1·5	13·0	0·5	5·0	20·0	*Nitzschia*
Aug.									
1	8·0	121	—	2·3	5·0	—	8·0	15·3	*Nitzschia* *Euglena*
8	—	90	—	1·0	14·0	—	1·0	16·0	—
16	8·2	113	—	10·5	31·5	—	10·5	52·5	*Chromulina pusilla*
24	—	80	—	—	9·0	—	7·5	16·5	—
31	8·1	51	—	1·0	32·0	—	4·5	37·5	—
Sept.									
9	—	38	—	0·5	11·5	—	6·0	18	*Pleurosigma*
14	8·05	108	—	1·0	13·5	—	4·0	18·5	Biraphideae and Centrales
26	8·0	129·5	—	—	8·5	—	2·5	11·0	—

V. SAMPLING OF OYSTER LARVAE

The method of pump sampling, used in the Oosterschelde for planktonic oyster larvae (Havir 1939; Korringa, 1941), is probably ideal for organisms which are numerous, sufficiently sr and compact to avoid damage in the pump, and not agile enough to escape the intake. A Ranso and Rapier $1\frac{1}{2}$ inch centrifugal pump was used at Burnham, with a short delivery hose and intake hose about 8 metres long, enabling samples to be pumped from various depths. It petrol driven and pumped at a very steady rate, delivering 100 litres in about half a min It was calibrated at the beginning of each season, and at intervals thereafter, by pumping a tank up to a mark which measured 100 l., its performance being timed with a stop-watch not varying by more than 4 seconds throughout the three years. Plankton samples, usuall 100 l., were obtained by pumping for appropriate periods through a plankton net (see frontispi which had a bucket with a detachable piece of bolting silk. After washing down, the silk placed in a jar with a small quantity of water which had been filtered through the net. In

aboratory the contents of each jar were tipped into a 20 centimetre evaporating dish, the silk insed and removed, formalin added to ensure that the larvae would sink, and the larvae concentrated y swirling and gradually pipetted out, counted and measured. Lengths were measured to the earest 0·01 mm. A special note was made of each larva possessing the pair of prominent eyespots eveloped towards the end of the planktonic stage, a sign that the larva is ready to settle.

The samples included numerous copepods and larvae of mollusca and crustacea, none of which ppeared to have been damaged by the pump. Most *Idotea linearis* and *Pleurobrachia pileus* vere mutilated, but a few specimens even of these relatively very large forms came through intact.

Korringa (1941) found that single 100 l. samples, taken daily at low water from two stations, ave a good record of larval abundance and growth in the Oosterschelde. He obtained evidence f fairly uniform vertical distribution during daytime. Loosanoff and Nomejko (1951) have riticised this method of sampling on the grounds that the larvae are not uniformly distributed, hough their own results obtained with it seem significant, giving a strong indication of breeding eriodicity. Certainly the larvae are not uniformly distributed, but the good agreement between he two series of samples from Korringa's stations shows that even a single series can give much nformation about events during a season. The variations which occur from place to place, hough great, seem to be generally less than those which occur from time to time, due to liberation nd disappearance of larvae. A few replicate samples at Burnham, taken at the same place and t the same depth, or at two different depths, also indicated that 100 l. constitute an adequate ample and that the depth of sampling is not important. The routine adopted in 1948 and 1949 vas to sample about every three days at three widely separated places in the Crouch and three n the Roach, at a depth of 2 metres. The samples from all three places in the same river showed imilar pictures of liberations and disappearance or growth of larvae (p. 21), which confirms hat this is an adequate method of sampling.

VI. SPAWNING PERIODICITY

Galtsoff (1930, 1932) showed that spawning in *Gryphaea virginica* and *G. gigas* is synchronised hrough the stimulating influence of sex products from individuals which spawn first. Such ehaviour has not been demonstrated in incubatory oysters, but Orton (1937) and Korringa (1941) pointed out that it probably occurs in *Ostrea edulis*, since well-marked spawning maxima have ften been observed. Orton (1926) opened weekly samples of oysters from the River Fal during 1925 and found two main spawning periods at times of full moon, but other similar investigations which he carried out did not show lunar periodicity. Nelson (1925) and Prytherch (1929) suggested that the periodicity observed by Orton might have been caused by greater changes in water emperature at spring tides, for when wide stretches of shore are exposed at low water the water will be warmed rapidly during fine weather. Korringa (1941) objected that prolonged fine weather is exceptional in England. Certainly at Burnham warming of the water and the extent of the fluctuations in temperature between high and low water depended on the weather and showed no correlation with the cycle of spring and neap tides. Korringa (1947) found that particularly large numbers of recently liberated larvae usually appeared about ten days after full moon and new moon. Since the incubation period is about eight days, this indicated spawning maxima about two days after full and new moon, i.e. at spring tides. The periodicity was probably linked to the tidal cycle, rather than the moonlight cycle, since it was not observed in tideless oyster breeding tanks (Cole, 1939) or the Limjford (Spärck, 1929).

Loosanoff and Nomejko (1951) questioned Korringa's conclusions on the grounds that they were based on single samples of 100 l., but this criticism was unjustified, as they were in fact based on sampling during nine years and therefore, in effect, on nine such samples. Moreover, records from French beds have shown similar periodicity. One can deduce times of neap tides from the first graph of larval abundance given by Herman (1938), in which most of the peaks occur at intervals of two weeks, and confirm them from the paper by Ladouce (1938) in the same journal.

Sampling at Burnham-on-Crouch in 1947 was rather infrequent and did not reveal any periodicity, but in 1948 numbers of recently liberated larvae from the Roach showed fortnightly peaks, which occurred about eight days after spring tides (Fig. 4). The only exception was a peak on 24th June, which indicated an exceptional spawning during the previous neap tides. Similar

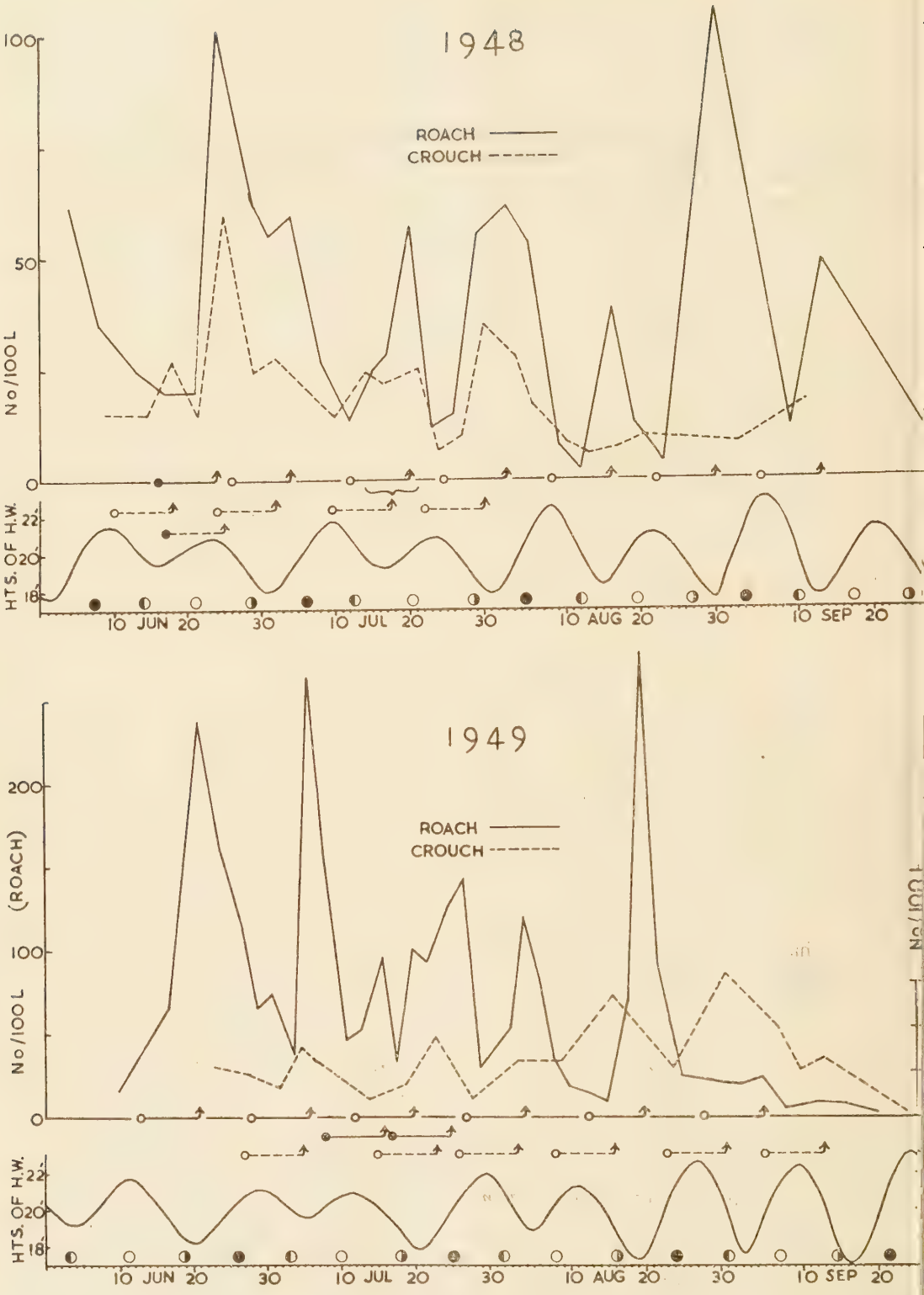


FIG. 4

Fluctuations in abundance of recently liberated larvae (less than ·22 mm. in length) correlated with cycles of spring and neap tides (heights of H.W. in feet at London Bridge). Increases in abundanc these larvae, which are indicated by arrows, probably followed mass spawnings about 8 days ea at times indicated by circles, since the incubation period is about 8 days. Most of these spawnings to have occurred during spring tides. The few exceptions which occurred at neap tides are indic by circles which have been blacked in.

eriodicity was observed in 1949, with a few exceptional, irregular peaks. Evidently spawning n Essex beds, as in the Oosterschelde, occurs more frequently at spring tides than at neap tides, ut goes on to some extent throughout the tidal cycle.

Those exceptional mass spawnings which occurred irregularly or at neap tides were not orrelated with abnormal tidal conditions. Observed heights of H.W. and L.W. at Southend-n-Sea near Burnham, kindly provided by the Port of London Authority, showed a close correlation vith the cycles given in Fig. 4, which are based on predicted heights taken from Brown's Nautical Almanack. There were no abnormally high or low tides associated with the exceptional mass pawnings.

The increased spawning activity at each period of spring tides probably results from conditions perating not at that particular period, but earlier. Korringa (1947) did not suggest that spawning s automatically induced at spring tides, by the greater pressure changes which occur then, though oosanoff and Nomejko (1951) apparently understood him to have done so. There is, of course, o evidence as to the precise nature of the link between breeding and tidal cycles or as to the time t which it operates. Oysters can probably perceive tidal changes in a variety of ways, especially hanges in current velocity and turbidity. Korringa pointed out that mass spawning must be receded by a period of roughly synchronous maturation of the gonads in a large number of ndividuals. This parallel development, culminating in spawning which is more closely synchronised hrough the stimulating influence of sex products from individuals which spawn first, must be ighly important in non-copulatory species, in ensuring fertilisation. It is not surprising to find ynchronisation effected by linking with the fortnightly tidal cycle, for Gompel (1938) has emonstrated a very well marked metabolic rhythm associated with the tides in a wide variety of narine animals. But the fortnightly spawning peaks are not due to fortnightly spawning by ndividual oysters. The majority of oysters spawn as females only once a season (Cole, 1941), o only a proportion of the total stock can contribute to each peak.

A possible advantage to be derived from this periodicity, in addition to spawning synchronisation, s that most larvae spend their first few days of independent life in conditions of minimum turbulence nd turbidity. The change from lecithotrophic to planktotrophic habits may well be a rather ritical one, for which optimum conditions are desirable. The breeding habits of several animals re so timed that this change generally occurs when tidal currents are at a minimum. Thus the viparous American oyster, *Gryphaea virginica*, shows a tendency to spawn mostly about the noon's quarters (Prytherch, 1929; Loosanoff and Nomejko, 1951) so the small larvae, reaching ne straight-hinge stage within three days, will generally begin to feed during neaps. Battle 1931, quoted by Korringa, 1947) found that *Mytilus edulis* and two other species of lamellibranch howed spawning peaks at full moon periods, the tidal range being uniformly low at that place nd time, except during the new moon spring tides. *Spirorbis borealis* regularly settles and adopts dult feeding habits during neap tides (Garbarini, 1933; Knight-Jones, 1951*c*). In this polychaete, n *Ostrea edulis*, and in the other lamellibranchs referred to above, it may roughly be estimated nat peak spawning occurs respectively 14, 8 and 3 days before the progeny have to seek their wn food, and the times taken for maturation must also vary in these different species, which have ggs of various sizes. Indeed their sexual cycles are vastly different, *Spirorbis borealis* producing ggs once a fortnight, *Ostrea edulis* about once a year. It is only when the young are launched n an independent life, during neap tides, that these cycles come into step, which supports the dea that this is a particularly critical time. In places where tidal currents are so slight as to be nimportant, breeding may be synchronised in some other way. Korringa (1947), explaining ow it is linked to the moonlight cycle in various littoral animals of nocturnal habits, showed nat the pelagic nuptial dances of *Platynereis dumerilii*, which occur during neap tides at Concarneau, vhere the tidal range is great, occur during full moon periods at Naples, where tides are very nall.

The link between oyster breeding and the tides helps in the prediction of periods when heavy patfalls are to be expected, though a spatfall depends as much on conditions being suitable for urvival and growth of larvae, as upon their abundant production.

VII. LIBERATION OF LARVAE DURING TIDAL CYCLE

The factors which influence oysters to liberate their larvae are not known: Korringa (194 found that liberations took place in all weathers and varying salinities, but the Burnham recor indicated that they do not occur with uniform frequency throughout the daily tidal cycles.

The routine samples of 1948 and 1949, which were taken regularly at three widely separat points in each river, showed that there were generally many more larvae in the lower reaches th the upper reaches. This might have followed from the distribution of parent stocks in the Crouc but not in the Roach. In the Roach parent stocks were concentrated in Paglesham Reach a adjoining creeks, within the area outlined in Fig. 7A. The lower reaches of the Roach contain practically no oysters, except for a small stock of young oysters in White House Hole. Oyst populations in the Crouch were very sparse compared with those in the Roach and fewer larv occurred in the Crouch samples than in the Roach samples. It follows that the majority of t larvae in the Roach samples must have been liberated by the numerous oysters which occurr in small, densely-populated areas in the upper reaches, near Paglesham.

If liberations occurred with uniform frequency in time throughout the tidal cycle, lar concentrations of larvae would appear in the water masses immobilised over oyster beds duri high slack water. As the tide began to ebb and increasingly larger volumes of water passed o the stocked areas in unit time, concentrations of larvae therein would decrease. As the ti slackened they would increase again and at low slack water peak concentrations would appe for the volume of water over the beds is much smaller at low water than at high water (Fig. 5).

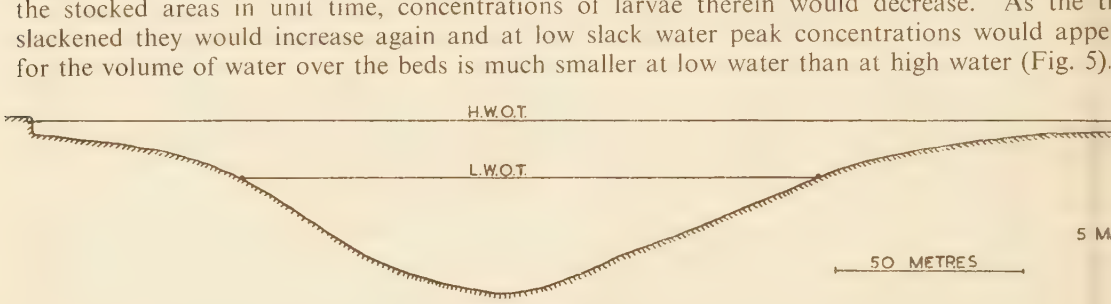


FIG. 5

A section across the River Roach at Paglesham (the vertical scale being four times the horizontal), show that the volume of water over grounds in this area, where the main oyster stocks lie, is nearly twice as g at high water as at low water. In spite of this, much greater concentrations of swimming larvae occu at high water.

On the contrary larvae were generally scarce in Paglesham Reach at low water (Table They were abundant there in samples taken at high water during 1948 and they were usu abundant in the water which was just within the mouth of the Roach at low water, most of wh must have been in the Paglesham area at high water (Fig. 7). They were especially numer in samples from White House Hole, of water which must have passed over the main parent sto when the tide was running fastest. Perhaps oysters are stimulated to liberate their larvae by gentle tidal currents which occur during neaps, for such behaviour would be adaptive, leadin increased dispersion of larvae and so reduced competition for food. It is difficult to underst why liberations should appear to take place more frequently at about high water than at al low water. Water temperatures were generally lower at high water than at low water (the differ being about 3° in sunny weather), but it seems unlikely that lowering of temperature would encou liberation. The thermograph records showed that there was usually a considerable ris temperature soon after high water, as the tide started ebbing. Perhaps this was responsible.

TABLE 5

Recently liberated larvae (<0·22 mm. long) per 100 l. at three stations in the River Roach during 1948 and 1949

At high water (during 1948 only) samples were taken from opposite Barton Hall Creek, Broadrakes and Paglesham Reach, at low water from Paglesham Reach, White House Hole and the mouth of the Roach (Fig. 1). The samples were therefore from water which moved with the tide over the upper, middle and lower reaches of the Roach respectively. Larvae were comparatively scarce in the water from the upper reaches, although this remained over the main breeding stocks, which were near Paglesham, during low slack water. Apparently liberations of larvae took place mainly at other stages of the tidal cycle.

HIGH WATER SAMPLES, 1948

Date	June					July			August			Mean
	4	8	21	24	29	4	17	20	5	16	19	
Upper	29	11	6	29	63	69	1	16	21	7	9	23·6
Middle	135	46	13	62	71	67	43	40	17	28	6	48·0
Lower	22	50	41	213	51	42	40	109	123	79	25	72·3

LOW WATER SAMPLES, 1948

Date	June		July							August					Mean
	13	17	1	8	12	15	23	26	29	2	9	12	23	30	
Upper	2	7	20	14	4	6	11	8	16	50	2	1	1	8	9·53
Middle	50	17	63	22	9	19	10	19	68	66	14	2	7	264	41·3
Lower	21	36	81	44	25	47	13	22	82	69	10	5	5	43	26·6

Date	1948 September			1949 June						July			Mean
	9	13	28	10	17	21	24	27	29	1	4	6	
Upper	0	11	3	1	60	83	91	81	50	96	44	71	49·3
Middle	6	61	6	17	91	447	205	193	108	108	27	365	136·2
Lower	31	75	13	29	52	288	189	58	38	22	41	357	99·4

Date	July										August				Mean
	8	11	13	16	18	20	22	25	27	29	2	4	6	8	
Upper	72	15	18	21	17	63	12	149	335	17	17	30	7	13	56·1
Middle	160	12	76	135	10	205	169	91	52	20	46	47	180	75	91·3
Lower	255	107	68	136	70	33	97	140	40	52	95	280	61	19	103·8

Date	August								September						Mean
	10	13	15	18	20	22	25	31	2	5	8	12	16	20	
Upper	7	5	1	18	41	17	19	6	2	3	1	1	5	0	9·0
Middle	9	15	0	32	487	174	28	24	42	20	5	7	7	3	60·9
Lower	39	26	22	159	288	78	26	30	11	45	11	17	8	1	54·3

Means of all samples:—Upper, 29·4; Middle, 75·7; Lower, 72·4.

VIII. SIZE, GROWTH AND SURVIVAL OF LARVAE

At the beginning of each season most of the smallest larvae, which may be presumed to hav been recently liberated, were about 0·20 mm. long. Later, smaller larvae appeared, measurin 0·18 or less (e.g. Tables 6, 7 and 8). Korringa (1941) found a similar phenomenon and rightl observed that there are no regular changes in temperature which might be responsible for it Probably oysters which produce larvae in the latter half of the season have depleted reserves o stored food, through earlier functioning as males. Cole (1941) found that later broods were les numerous than earlier ones, probably for this reason, so it is not surprising to find evidence tha they generally consist of smaller larvae.

TABLE 6A

Numbers of oyster larvae in 100 l. plankton samples from the middle reaches of the Roach during 1948. On dates marked (*) samples were from Broadrakes (Fig. 1) at H.W.: remainder were from White House Hole at L.W.

Date	Total larvae	Size distribution (mm.) ·17	·18	·19	·20	·21	·22	·23	·24	·25	·26	·27	·28	·29	·30	·31	Eyed larvae
1948 June																	
4*	161	—	—	—	68	67	23	3	—	—	—	—	—	—	—	—	—
8*	71	—	—	—	19	27	14	8	3	—	—	—	—	—	—	—	—
13	54	—	1	8	19	19	7	—	—	—	—	—	—	—	—	—	—
17	45	—	1	2	4	10	18	5	3	2	—	—	—	—	—	—	—
21*	32	—	1	1	5	6	5	3	5	3	3	—	—	—	—	—	—
24*	79	—	2	7	30	23	11	—	2	2	—	1	1	—	—	—	2
29*	156	—	2	1	17	51	43	22	12	2	4	2	—	—	—	—	4
July																	
1	138	—	—	1	16	46	24	27	13	8	2	—	—	1	—	—	1
4*	114	—	3	5	38	21	15	6	21	—	1	1	1	1	1	—	4
8	26	—	—	3	10	9	4	—	—	—	—	—	—	—	—	—	—
12	17	—	—	—	4	5	4	2	1	1	—	—	—	—	—	—	—
15	27	—	—	5	9	5	6	1	1	—	—	—	—	—	—	—	—
17*	53	—	—	5	16	22	8	—	—	2	—	—	—	—	—	—	—
20*	75	—	7	7	14	12	5	9	16	3	—	2	—	—	—	—	
23	18	—	—	—	2	8	4	2	1	1	—	—	—	—	—	—	—
26	35	—	—	4	4	11	7	4	3	2	—	—	—	—	—	—	—
29	100	—	—	4	38	26	22	7	3	—	—	—	—	—	—	—	—
Aug.																	
2	234	—	1	3	23	39	27	19	27	20	30	19	12	9	4	1	2
5*	69	—	—	—	5	12	10	5	3	8	2	3	7	10	4	—	2
9	19	—	—	3	3	9	3	—	—	1	—	—	—	—	—	—	—
12	3	—	—	—	1	1	—	—	—	1	—	—	—	—	—	—	—
16*	31	—	5	10	7	5	2	1	1	—	—	—	—	—	—	—	—
19*	7	—	—	3	2	1	—	—	—	1	—	—	—	—	—	—	—
23	8	—	2	2	2	1	1	—	—	—	—	—	—	—	—	—	—
30	316	9	50	82	91	32	32	14	4	—	2	—	—	—	—	—	—
Sept.																	
9	7	—	1	1	3	1	1	—	—	—	—	—	—	—	—	—	
13	67	—	10	20	23	8	2	2	2	—	—	—	—	—	—	—	—
28	7	—	2	4	—	—	—	1	—	—	—	—	—	—	—	—	—

TABLE 6B

As in Table 6A, but from the lower reaches of the Roach. On dates marked (*) samples were from Paglesham Reach at H.W.: remainder were from just inside the mouth of the Roach at L.W.

Date	Total larvae	Size distribution (mm.) ·17	·18	·19	·20	·21	·22	·23	·24	·25	·26	·27	·28	·29	·30	·31	Eyed larvae
1948																	
June																	
4*	25	—	—	—	10	12	3	—	—	—	—	—	—	—	—	—	—
8*	73	—	—	2	13	35	15	7	—	—	1	—	—	—	—	—	—
13	30	—	1	2	6	12	7	1	—	1	—	—	—	—	—	—	—
17	92	—	—	2	10	24	30	15	4	2	4	1	—	—	—	—	—
21*	91	—	1	1	25	14	7	14	15	6	3	2	3	—	—	—	3
24*	297	—	22	23	89	79	36	36	1	5	2	3	—	—	1	—	1
29*	92	—	—	9	13	29	26	9	3	—	—	3	—	—	—	—	1
July																	
1	186	—	1	2	42	36	15	21	26	31	10	—	—	1	1	—	2
4*	74	—	1	4	22	15	9	12	5	4	1	1	—	—	—	—	1
8	67	—	1	3	25	15	12	6	2	—	—	3	—	—	—	—	2
12	30	—	1	8	8	8	4	1	—	—	—	—	—	—	—	—	—
15	54	—	2	8	25	12	5	2	—	—	—	—	—	—	—	—	—
17*	50	—	2	6	23	9	6	4	—	—	—	—	—	—	—	—	—
20*	171	—	4	11	54	40	29	18	7	6	1	1	—	—	—	—	—
23	19	—	—	3	5	5	4	—	2	—	—	—	—	—	—	—	—
26	48	—	—	2	8	12	2	1	10	1	5	5	2	—	—	—	—
29	125	—	1	13	30	38	24	13	1	1	1	—	1	—	2	—	2
Aug.																	
2	309	—	1	2	25	41	34	38	28	32	31	34	31	7	5	—	17
5*	183	—	20	29	43	31	26	14	3	—	3	3	5	3	2	1	13
9	12	—	—	3	5	2	1	—	—	—	—	1	—	—	—	—	1
12	5	—	—	1	1	3	—	—	—	—	—	—	—	—	—	—	—
16*	85	—	5	31	38	5	2	2	—	1	1	—	—	—	—	—	—
19*	26	—	8	6	11	—	—	1	—	—	—	—	—	—	—	—	—
23	5	—	1	3	1	—	—	—	—	—	—	—	—	—	—	—	—
30	43	2	17	16	8	—	—	—	—	—	—	—	—	—	—	—	—
Sept.																	
9	33	1	2	17	10	1	1	—	—	1	—	—	—	—	—	—	—
13	82	2	5	29	23	16	—	2	5	—	—	—	—	—	—	—	—
28	14	—	—	2	8	3	1	—	—	—	—	—	—	—	—	—	—

TABLE 7A

Numbers of oyster larvae in 100 l. plankton samples from the middle reaches of the Roach, i.e. White House Hole at L.W., during 1949

Date	Total larvae	Size distribution (mm.) ·16	·17	·18	·19	·20	·21	·22	·23	·24	·25	·26	·27	·28	·29	·30	·31	Eyed larvae
1949																		
June																		
10	33	—	—	—	—	8	9	8	6	2	—	—	—	—	—	—	—	—
17	165	—	—	—	9	42	40	45	19	5	3	1	1	—	—	—	—	—
21	877	—	—	12	67	165	203	116	110	87	68	27	13	7	2	—	—	5
24	555	—	—	—	11	75	119	103	97	65	43	17	14	8	1	1	1	10
27	616	—	—	17	11	99	68	96	119	65	59	17	29	34	—	1	1	4
29	335	—	—	10	3	45	60	57	60	45	16	16	8	3	7	3	2	19
July																		
1	193	—	—	5	28	38	37	21	23	21	7	9	3	—	—	1	—	2
4	41	—	—	—	11	8	8	6	8	—	—	—	—	—	—	—	—	—
6	441	—	7	30	163	133	32	22	15	15	19	3	2	—	—	—	—	5
8	196	—	3	13	32	75	21	16	19	6	4	6	1	—	—	—	—	7
11	53	—	—	—	8	4	21	8	12	—	—	—	—	—	—	—	—	—
13	106	—	2	5	11	41	17	11	12	2	2	3	—	—	—	—	—	2
16	145	—	7	17	17	59	35	—	—	3	7	—	—	—	—	—	—	—
18	28	—	—	—	3	3	4	11	4	—	3	—	—	—	—	—	—	—
20	236	4	9	32	60	87	13	11	4	2	10	2	2	—	—	—	—	—
22	306	—	3	23	29	54	60	71	26	11	11	9	—	6	3	—	—	9
25	114	2	5	19	23	29	13	12	3	3	—	3	—	2	—	—	—	2
27	65	2	—	7	12	14	17	7	4	—	—	1	1	—	—	—	—	2
29	25	—	2	6	5	7	—	2	2	—	—	—	1	—	—	—	—	1
Aug.																		
2	46	3	6	20	10	5	2	—	—	—	—	—	—	—	—	—	—	—
4	48	—	—	—	20	16	11	—	—	—	—	—	1	—	—	—	—	1
6	194	—	—	43	78	38	21	10	2	1	1	—	—	—	—	—	—	—
8	96	—	2	12	23	19	19	13	4	2	1	1	—	—	—	—	—	1
10	10	—	—	1	5	2	1	1	—	—	—	—	—	—	—	—	—	—
13	15	1	1	5	6	2	—	—	—	—	—	—	—	—	—	—	—	—
18	36	—	—	8	12	8	4	4	—	—	—	—	—	—	—	—	—	—
20	520	—	11	55	153	246	22	11	—	22	—	—	—	—	—	—	—	—
22	239	—	—	12	47	53	62	27	26	9	—	2	1	—	—	—	—	—
25	35	—	—	2	10	8	8	3	2	2	—	—	—	—	—	—	—	—
31	28	1	3	4	13	3	4	—	—	—	—	—	—	—	—	—	—	—
Sept.																		
2	43	—	4	9	20	6	3	1	—	—	—	—	—	—	—	—	—	—
5	26	—	—	3	4	7	6	4	1	—	1	—	—	—	—	—	—	—
8	7	—	—	1	1	3	—	1	1	—	—	—	—	—	—	—	—	—
12	7	—	—	—	2	3	—	1	—	—	1	—	—	—	—	—	—	1
16	7	—	—	2	4	1	—	—	—	—	—	—	—	—	—	—	—	—
20	3	—	—	—	1	2	—	—	—	—	—	—	—	—	—	—	—	—

TABLE 7B

As in Table 7A, but from the lower reaches, i.e. just within the mouth of the Roach at L.W.

Date	Total larvae	Size distribution (mm.)																Eyed larvae
		·16	·17	·18	·19	·20	·21	·22	·23	·24	·25	·26	·27	·28	·29	·30	·31	
949																		
une																		
10	51	—	—	—	2	9	18	11	9	2	—	—	—	—	—	—	—	—
17	86	—	—	—	2	15	35	24	7	—	3	—	—	—	—	—	—	—
21	616	—	—	—	24	142	122	103	93	69	39	10	11	2	—	1	—	4
24	615	—	—	18	28	65	78	111	124	69	60	20	27	10	3	2	—	12
27	117	—	—	6	3	23	26	25	6	3	6	9	3	3	3	1	—	4
29	80	—	—	2	7	17	12	14	9	11	2	2	3	1	—	—	—	2
uly																		
1	39	—	—	—	2	10	10	4	—	4	2	5	1	—	1	—	—	3
4	62	—	—	9	9	14	9	10	3	3	4	—	1	—	—	—	—	2
6	528	—	18	18	113	125	83	60	66	25	14	2	3	—	1	—	—	9
8	327	—	—	28	74	79	74	56	12	—	2	—	1	1	—	—	—	4
11	134	—	—	11	11	45	40	11	6	1	6	1	2	—	—	—	—	3
13	101	—	2	—	18	28	20	14	—	8	9	2	—	—	—	—	—	6
16	157	—	3	13	46	57	17	10	3	7	—	—	1	—	—	—	—	1
18	136	—	3	3	6	37	21	30	9	12	6	6	3	—	—	—	—	—
20	48	—	1	5	11	7	9	8	3	1	1	2	—	—	—	—	—	—
22	136	—	7	28	25	22	15	12	10	—	—	10	7	—	—	—	—	11
25	195	—	10	25	33	52	20	10	13	5	20	2	1	2	2	—	—	7
27	44	—	4	9	14	9	4	2	2	—	—	—	—	—	—	—	—	—
29	55	1	2	14	14	16	5	1	1	1	—	—	—	—	—	—	—	—
ug.																		
2	96	—	8	47	24	12	4	—	—	—	1	—	—	—	—	—	—	1
4	308	—	12	79	115	60	14	17	7	1	1	1	1	—	—	—	—	3
6	64	—	—	8	23	18	12	—	3	—	—	—	—	—	—	—	—	—
8	23	—	—	3	5	6	5	3	—	—	1	—	—	—	—	—	—	—
10	45	—	2	8	14	12	3	5	—	1	—	—	—	—	—	—	—	—
13	26	—	3	7	13	3	—	—	—	—	—	—	—	—	—	—	—	—
15	22	—	—	4	13	3	2	—	—	—	—	—	—	—	—	—	—	—
18	170	—	6	46	39	29	39	6	3	—	—	—	—	2	—	—	—	2
20	314	—	15	41	113	83	36	21	5	—	—	—	—	—	—	—	—	—
22	87	—	3	27	23	13	12	2	4	2	—	1	—	—	—	—	—	—
25	36	—	1	2	7	12	4	6	1	—	2	1	—	—	—	—	—	3
31	34	—	—	6	13	9	2	4	—	—	—	—	—	—	—	—	—	—
ept.																		
2	13	—	—	1	2	6	2	1	1	—	—	—	—	—	—	—	—	—
5	58	—	3	4	8	15	15	8	3	—	1	—	1	—	—	—	—	2
8	14	—	—	1	6	4	—	—	1	1	—	1	—	—	—	—	—	1
12	17	—	2	3	6	3	3	—	—	—	—	—	—	—	—	—	—	—
16	8	—	—	2	5	—	1	—	—	—	—	—	—	—	—	—	—	—
20	1	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—

TABLE 8A

Numbers of oyster larvae in 100 l. plankton samples from the Crouch opposite the mouth of Althorne Creek (Fig. 1) at L.W. during 1949

Date	Total larvae	Size distribution (mm.) ·16	·17	·18	·19	·20	·21	·22	·23	·24	·25	·26	·27	·28	·29	Eye lar
1949																
June																
23	28	—	—	—	—	5	7	13	2	—	1	—	—	—	—	—
28	5	—	1	—	—	—	2	1	1	—	—	—	—	—	—	—
July																
2	9	—	—	1	1	1	2	2	1	1	—	—	—	—	—	—
5	14	—	—	3	3	6	2	—	—	—	—	—	—	—	—	—
7	34	—	—	3	3	11	8	6	1	—	1	—	—	1	—	—
14	4	—	—	—	1	2	—	1	—	—	—	—	—	—	—	—
19	6	—	1	1	2	1	1	—	—	—	—	—	—	—	—	—
23	21	—	1	5	5	5	1	4	—	—	—	—	—	—	—	—
28	10	—	—	—	1	—	2	3	1	1	—	1	1	—	—	—
Aug.																
3	24	—	—	8	6	4	2	1	2	1	—	—	—	—	—	—
9	9	—	—	1	1	—	4	3	—	—	—	—	—	—	—	—
16	41	2	—	6	14	8	5	5	—	—	1	—	—	—	—	—
24	18	—	1	5	4	2	1	2	1	—	2	—	—	—	—	—
31	48	—	—	5	8	8	9	8	5	3	2	—	—	—	—	—
Sept.																
7	23	—	1	1	1	6	2	—	1	2	2	2	4	1	—	
10	14	—	—	—	2	2	3	1	3	2	1	—	—	—	—	
13	19	—	—	4	7	5	1	1	1	—	—	—	—	—	—	—

TABLE 8B

As in Table 8A, but from opposite Burnham at L.W.

Date	Total larvae	Size distribution (mm.) ·17	·18	·19	·20	·21	·22	·23	·24	·25	·26	·27	·28	Eyed larva
1949														
June														
23	28	—	—	—	4	10	9	3	—	1	1	—	—	—
28	70	—	2	2	8	8	25	16	6	—	3	—	—	1
July														
2	13	—	4	2	3	1	1	—	—	—	1	1	—	2
5	38	—	1	10	14	7	4	1	—	1	—	—	—	—
7	4	—	—	2	1	—	—	1	—	—	—	—	—	—
14	6	—	1	2	2	—	—	—	—	1	—	—	—	—
19	8	2	1	3	2	—	—	—	—	—	—	—	—	—
23	51	—	—	2	11	19	8	6	—	2	1	1	1	3
28	7	—	—	—	1	—	1	1	1	2	1	—	—	1
Aug.														
3	28	1	2	10	8	—	1	2	1	1	1	—	1	2
9	27	1	11	8	7	—	—	—	—	—	—	—	—	—
16	30	3	8	3	11	3	—	—	—	2	—	—	—	—
24	18	1	3	4	—	4	4	—	—	—	1	1	—	2
31	57	—	6	9	10	17	8	6	1	—	—	—	—	—
Sept.														
7	56	—	3	2	3	4	8	10	9	8	4	3	2	10
10	25	—	6	3	2	1	7	—	1	1	3	1	—	5
13	22	—	2	4	6	3	2	2	2	—	1	—	—	1

When a larva has reached the end of the planktonic stage and is about to metamorphose, develops for the first time a pair of black pigment spots (Erdmann, 1934), which can be seen asily through the transparent shell and which must be regarded on morphological grounds as mple eyes (Cole, 1938*a*). Eyed larvae varied in size, but were usually between 0·26 and 0·30 mm. ong. In 1949, when prolonged fine weather allowed growth throughout the summer, eyed larvae om later samples were markedly smaller than those from earlier samples (Table 9). Two measured nly 0·23, several measured 0·24 and some which settled on slates in the Crouch during September easured just under 0·25 mm. The majority of these particularly small larvae were derived from te-spawning parents, which liberated small larvae. In 1948 eyed larvae occurred only in the arlier half of the season, all were derived from larvae which had been liberated at a fairly large ze, and all were at least 0·26 mm. The smallest eyed larvae which have been recorded previously, far as I am aware, were about 0·255 mm. (Cole, 1939; Korringa, 1941).

TABLE 9

Decrease in the size at which larvae reached the stage of metamorphosis as the 1949 season progressed, as shown by measurements of eyed larvae from the 100 l. samples

Numbers of eyed larvae in each 0·01 mm. size group:—

Month	·23	·24	·25	·26	·27	·28	·29	·30	·31mm.
ne	—	—	—	5	18	24	21	12	4
ly	1	3	14	35	30	14	7	1	—
igust	—	3	11	5	4	3	—	—	—
ptember	1	2	12	12	10	3	—	—	—

In 1948 eyed larvae from the upper reaches tended to be slightly smaller than those from the iddle and lower reaches of the Crouch and Roach during the same period (Fig. 6). This may ave been due to precocious development at higher temperatures, for at that time the water was or 3° warmer in the upper reaches than in the lower reaches. Early in 1949, when the numerous ed larvae from the Upper Roach were similar in size to those from the lower reaches, temperature fferences between the upper and lower reaches were slight and inconsistent. An inverse relation tween the size reached by organisms and the temperature of development seems fairly general, d Norris, Jones, Lovegrove and Crisp (1951) have noticed that barnacle larvae which have veloped under colder conditions reach a rather larger size.

Tables 6, 7 and 8 illustrate how measurement of larvae in successive 100 l. samples indicated hether the bulk of the larval population was growing or dying. On most dates in 1948 larvae rger than 0·22 mm. were scarce or absent, showing that little or no growth had been taking place, t periodically successive samples showed gradually increasing numbers of larger larvae. Such idence of good growth and survival appeared at similar times in the two series of samples shown Table 6, and also in four parallel series taken during 1948 at one other station in the Roach d three in the Crouch. Evidently the method of sampling was adequate for revealing periods vourable for growth. Samples taken during 1949 at three stations in the Roach also showed od agreement amongst themselves. Two of these series are given in Table 7. Less frequent mpling at three stations in the Crouch, of which two are given in Table 8, showed a course of ents similar at all three stations, but quite different from that in the Roach.

Korringa (1941) found evidence that the duration of the planktonic stage was less than a week water temperatures exceeding 22° C and more than two weeks at temperatures below 17° C. e Burnham records indicate similar variations in rate of growth. Thus in 1948 the gradually creasing size of the largest larvae between the 13th and 24th of June (Table 6) suggests that the vae which were ripe for metamorphosis on the 24th had measured less than 0·22 mm. on the th, pointing to a planktonic life of perhaps 11 days at 17°–18°; yet the large numbers of eyed vae, present in the samples of the 2nd of August, had probably measured 0·22 mm. or less the 29th and had not been liberated on the 26th, so their planktonic life appears to have been s than a week, at 22°–23°. But it is unlikely that temperature is the only factor affecting the ration of the planktonic phase. Food is probably also important. Whereas experiments in all vessels showed growth to settlement size on a diet of flagellates within two weeks, similar vae without suitable food remained swimming for a similar period without showing the slightest

growth (Cole, 1939). Probably a scanty food supply will allow slow growth. Certainly t conditions which lead to high temperatures also favour the production of food organisms.

The Burnham records showed that here, as in the Oosterschelde (Korringa, 1941), only a sm percentage of larvae survive to the stage of metamorphosis. Recently liberated larvae, less th 0·22 mm. in length, were generally much the most numerous. Larvae showing good grow (e.g. larger than 0·24 mm.) were comparatively scarce and eyed larvae still scarcer. Table gives the mean numbers per 100 l. of larvae falling into these three developmental categori The percentages of recently liberated larvae reaching the eyed stage were only about 1 in 19 8 in 1948 and 5 in 1949.

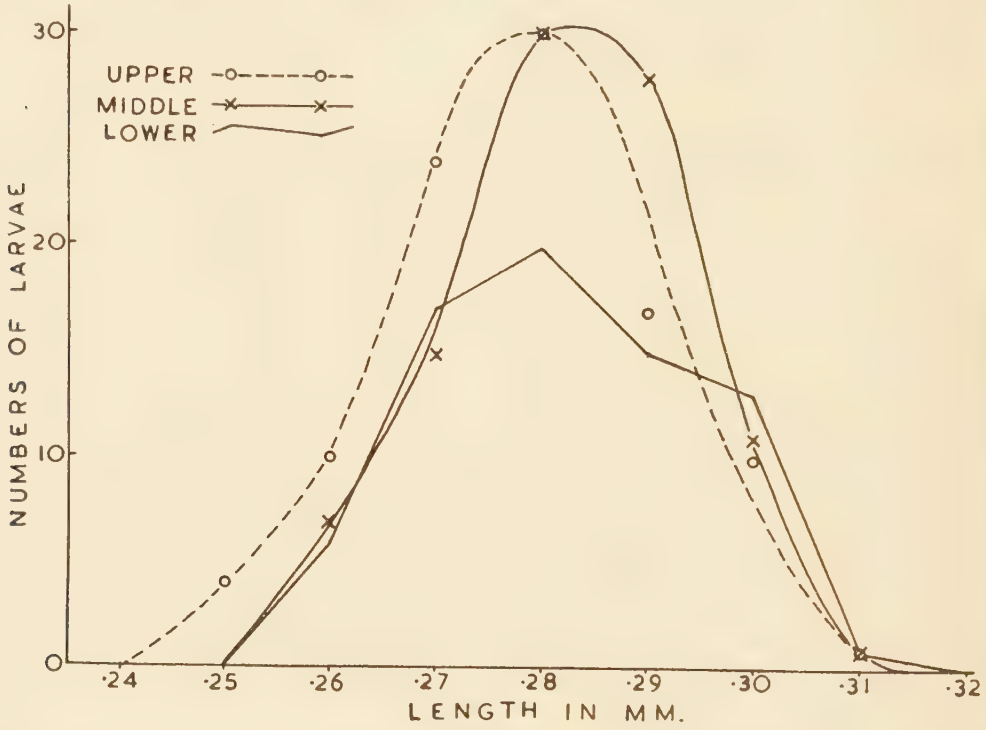


FIG. 6

The size distributions of all eyed larvae in routine samples from the upper, middle and lower reac of the Crouch and Roach during 1948. Samples from the upper reaches contained significantly m smaller eyed larvae.

It is more difficult to obtain figures showing short-term fluctuations in survival rate through the season. These fluctuations were very great, particularly in 1948, when the weather changeable. Throughout most of that season large larvae were very scarce (Table 6) and n of the liberation peaks shown in Fig. 4 were not followed by any settlement of spat. A percentage survival appeared about the end of June and a very high percentage in the week follow 29th July. Table 11 shows consecutive pairs of samples taken during this week from vari stations. The samples taken on 2nd and 3rd August contained a total of 98 eyed larvae, a still greater number of larvae which were almost as large, but which lacked eyespots. It is n unlikely that the eyed stage can be reached in less than four days, so probably the eyed la were derived from the populations of small larvae represented in the samples taken four earlier. There were only 309 larvae of all sizes in the earlier samples, so it seems that over 30 cent of these survived to the eyed stage. This is probably a considerable underestimate, for of the larvae in the earlier samples measured 0·21 or less. It is doubtful whether these ne liberated larvae could have completed their development in so short a time as four days and quite likely that they were represented in the later samples by the numerous large larvae w still lacked eyespots. No doubt many of these completed their development later (eyed la were still abundant in samples taken on 5th August), so the survival rate during this brief pe may well have exceeded 50 per cent. A remarkably intensive spatfall occurred within the few days, the yield from which far exceeded that from the whole of the remainder of the sea

TABLE 10

Mean numbers per 100 l. of larvae, which were (a) recently liberated, (b) well-grown and (c) ready to settle, observed during routine sampling in the three seasons. In the right-hand columns (b) and (c) are expressed as percentages of (a) to give a general index of survival and growth (but see p. 25).

—	(a) <0·22 mm.	(b) >0·24 mm.	(c) eyed	(b) as percentage of (a)	(c) as percentage of (a)
1947					
Roach	36·1	1·41	0·39	3·9	1·1
Lower Crouch	15·9	0·27	0·10	1·7	0·6
Upper Crouch	3·41	0·12	0·06	3·5	1·8
1948					
Upper Roach	15·1	4·86	2·00	32·1	13·2
Middle Roach	44·0	6·39	2·14	14·5	4·9
Lower Roach	50·6	9·75	1·54	19·3	3·0
Lower Crouch	29·2	6·0	1·55	20·5	5·3
Middle Crouch	15·7	4·4	1·39	28·0	8·8
Upper Crouch	12·0	4·31	1·74	36·0	14·5
1949 (all L.W.)					
Paglesham	40·25	5·58	1·05	13·8	2·6
Wh. Ho. Hole	99·5	17·25	1·92	17·3	1·9
Roach Mouth	88·9	9·66	2·24	10·9	2·5
Burnham	16·4	2·56	1·56	15·5	9·5
Althorne	12·7	1·00	0·89	7·9	7·0
Fambridge	7·94	0·69	0·75	8·7	9·4

TABLE 11

Evidence of extraordinarily high rates of survival of oyster larvae between 29 July and 3 August, 1948, given by consecutive 100 l. plankton samples from various stations. As usual, the greatest concentrations of recently liberated larvae occurred in the lower and middle reaches of the Roach (p. 14) but larvae which were approaching the end of their planktonic life had become widely distributed (p. 25).

Stations and dates	Numbers per 100 l. of larvae measuring:— ·18	·19	·20	·21	·22	·23	·24	·25	·26	·27	·28	·29	·30	·31	Total larvae on earlier date	Eyed larvae on later date
Lower Roach																
July 29	1	13	30	38	24	13	1	1	1	—	1	—	2	—	125	—
Aug. 2	1	2	25	41	34	38	28	32	31	34	31	7	5	—	—	17
Middle Roach																
July 29	—	4	38	26	22	7	3	—	—	—	—	—	—	—	100	—
Aug. 2	1	3	23	39	27	19	27	20	30	19	12	9	4	1	—	25
Upper Roach																
July 29	—	—	3	12	9	4	3	—	—	—	—	—	—	—	31	—
Aug. 2	—	4	19	27	32	21	19	8	9	6	8	6	1	—	—	18
Middle Crouch																
July 30	—	—	4	11	10	4	3	4	—	—	1	—	—	—	37	—
Aug. 3	—	5	18	22	12	5	4	11	3	8	6	6	2	—	—	20
Upper Crouch																
July 30	—	—	3	4	3	2	1	1	—	—	1	1	—	—	16	—
Aug. 3	—	—	5	17	8	9	7	9	5	8	5	2	1	—	—	18
															309	98

IX. DISTRIBUTION OF BREEDING STOCKS AND OF LARVAE

The distribution of breeding oysters in the Crouch and Roach, during the period under review, was very unequal because of the heavy mortality following the extraordinarily severe winter weather, which continued from 20th January to 4th March 1947. Dredge hauls in the lower reaches of the Crouch during the spring of 1947 contained about ten pairs of clean dead valves to every live oyster, pointing to a mortality of more than 90 per cent. Up river the mortality was even higher and not a single live oyster could be found above Bridgemarsh Island (Fig. 7A). In the well-stocked Paglesham area the mortality was probably about 90 per cent, further down the Roach there were few oysters, and below White House Hole there was practically none, since the muddy bottom there is too soft.

Stocks began to be built up again gradually in the Paglesham area, as local oystermen carried on their usual practice of laying dense concentrations of oysters there, on shallow grounds which are particularly favourable for growth and from which recovery for sale is easy. The oysters were obtained partly from Brittany and partly by dredging, from the middle and lower reaches of the Crouch, the sparse survivors of the severe winter. Thus there accumulated near Paglesham, by the summer of 1947, stocks totalling between half a million and a million oysters at least two years old. During each winter many of the larger oysters were removed for sale, but continued relaying of young oysters more than compensated for this, until in 1949 there must have been more than a million relaid oysters at least two years old, in addition to perhaps an equivalent number derived from the poor spatfall of 1947.

Oysters spatted in 1947 probably contributed to the comparatively large concentrations of larvae in the Roach during 1949, but the 1947 spatfall was practically confined to the Paglesham area, so did not help appreciably to stock the Crouch. In the Crouch there were only scattered, naturally-occurring oysters, the majority in Cliff Reach and near the mouth of the Roach, and some small but densely laid experimental patches on the Ministry's grounds (Fig. 1), each of about 10,000 oysters from the Conway breeding tanks. Widely dispersed oysters probably do not breed normally (Orton, 1927). The 1948 spatfall was well distributed throughout the Crouch and Roach, but these oysters were probably too small to breed early in 1949, though the late spawning in the Crouch during 1949 may well have been due to this year class. Earlier in 1949 larvae were scarcer in the Crouch than in 1948.

As tidal currents at Burnham were evidently strong enough to sweep planktonic larvae several miles in a few hours, experiments were carried out with drifting indicators to discover their horizontal amplitude. A bucket was suspended in mid-channel, at a depth of two metres from a small float, and allowed to drift for six hours, from one slack water period to the next. It was accompanied

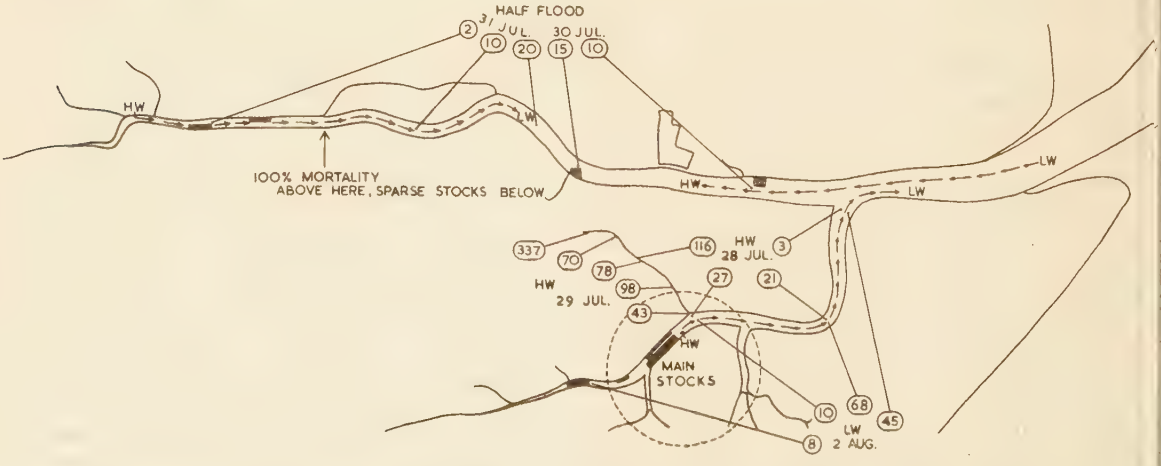
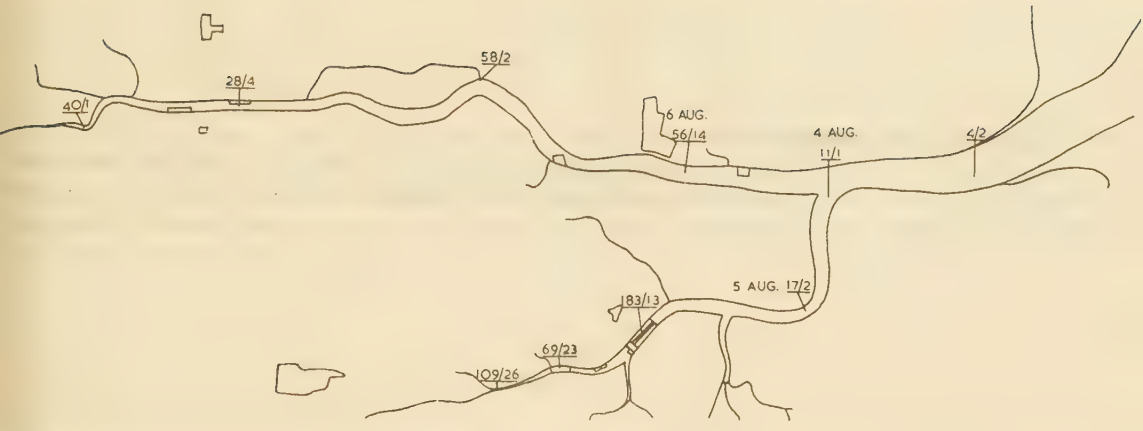


FIG. 7

A. Tidal currents and the distribution of larvae at the time of the main spatfall of 1947. Chains of arrows show distances covered by drifting indicators between successive slack water periods. A dotted circle encloses the area in which the main stocks of breeding oysters lay. All oysters in the upper reaches of the Crouch had died during the previous severe winter. The numbers in circles are of larvae per 100 l. on the dates and at the states of tide given.



3. Numbers of larvae of all sizes and numbers of eyed larvae in 100 l. samples taken at H.W. on the dates given, which were about the time of the main spatfall of 1948.

by a boatman, who replaced it in mid-stream on the few occasions when it grounded. Three experiments were carried out, in three different places, each on a tide intermediate between springs and neaps. They showed that moderate tides can transport larvae about five miles in six hours, so that larvae which are liberated near Paglesham at high water can be carried down to the Crouch on the ebb and back to Cliff Reach on the next flood. Evidently a planktonic stage lasting a week allows wide dispersion.

Plankton sampling in all three years showed concentrations of larvae in the Roach several times as great as those in the Crouch. At low water the highest concentrations in both rivers were in the lower reaches near the mouth of the Roach (Table 10), so many of the numerous larvae in the Roach must have been swept out into the Crouch at low water. Fig. 7 shows the results of surveys of larval abundance carried out at the times of the main spatfalls in 1947 and 1948. In 1947 particularly high concentrations of larvae (over three per litre) occurred in the headwaters of well-stocked creeks such as Paglesham Pool, but these were practically all small larvae, which had evidently just been liberated and were probably soon dispersed. Larvae occurred throughout the Crouch from the mouth to at least two miles above Fambridge, but only in small concentrations. Large larvae were too sparse to appear regularly in 100 litres. In 1948 larvae of all sizes were abundant and widely distributed. In 1949 the tendency for the larval population of the Roach to be concentrated in the lower reaches was not quite so marked as in 1948 (Table 10). It appeared that the high concentrations in the Roach during 1949 were to a larger extent retained there and that concentrations in the Crouch were correspondingly lower.

Table 10 shows that the highest percentages of eyed larvae generally occurred in the headwaters. This was probably due in part to more rapid development and better survival (here (p. 21), but must have been largely due to the fact that these waters contained comparatively few recently liberated larvae and hence a large proportion of those which had been swimming longest, and which had become dispersed. Carriker (1951) suggested that large larvae of *Gryphaea virginica* tend to drop to the bottom during the ebb and rise again on the flood, so that they get carried up river, but the basis for this idea was slight, for it was only in one 50 l. sample that he found many large larvae near the bottom during the ebb. In the Crouch larvae seemed to be gradually dispersed both up and down river, for occasional samples near the mouth at high water showed a high proportion of large larvae amongst the few larvae which occurred there.

X. INTENSITY AND DISTRIBUTION OF SPATFALL

Evidence of the progress and distribution of the spatfall was obtained by exposing smooth slates for weekly periods just below low water of spring tides on each of the Ministry's grounds and at certain other places (Fig. 8). The slates were held horizontally about 5 cm. above the surfaces of concrete slabs, which rested on the bottom. Each slate was held only by four thin upright bolts, so that movement of water over its surface was unrestricted (as in Fig. 1 of Knight-Jones and Stephenson, 1950). The slabs had ropes attached, which were fastened to buoys or tall saplings and prevented from fouling the slates by hoops of stiff wire, which had their ends embedded

in the concrete. Most of the slabs held two slates, one of which was changed weekly, whilst th other was left unchanged throughout the season. The slates measured 25 × 18 cm., but fc laboratory counts of attached organisms a counting frame was used which covered a central are of 212 cm^2. Counts of the upper and lower surfaces of each slate therefore covered 424 cm^2.

The periods of exposure of slates and numbers of oyster spat recorded at each station durin the three seasons are given in Fig. 8. The results for neighbouring stations indicate the times a which spatfall peaks occurred, and these coincided with the appearance of peak numbers of eye larvae in the plankton samples (Figs. 11 to 15).

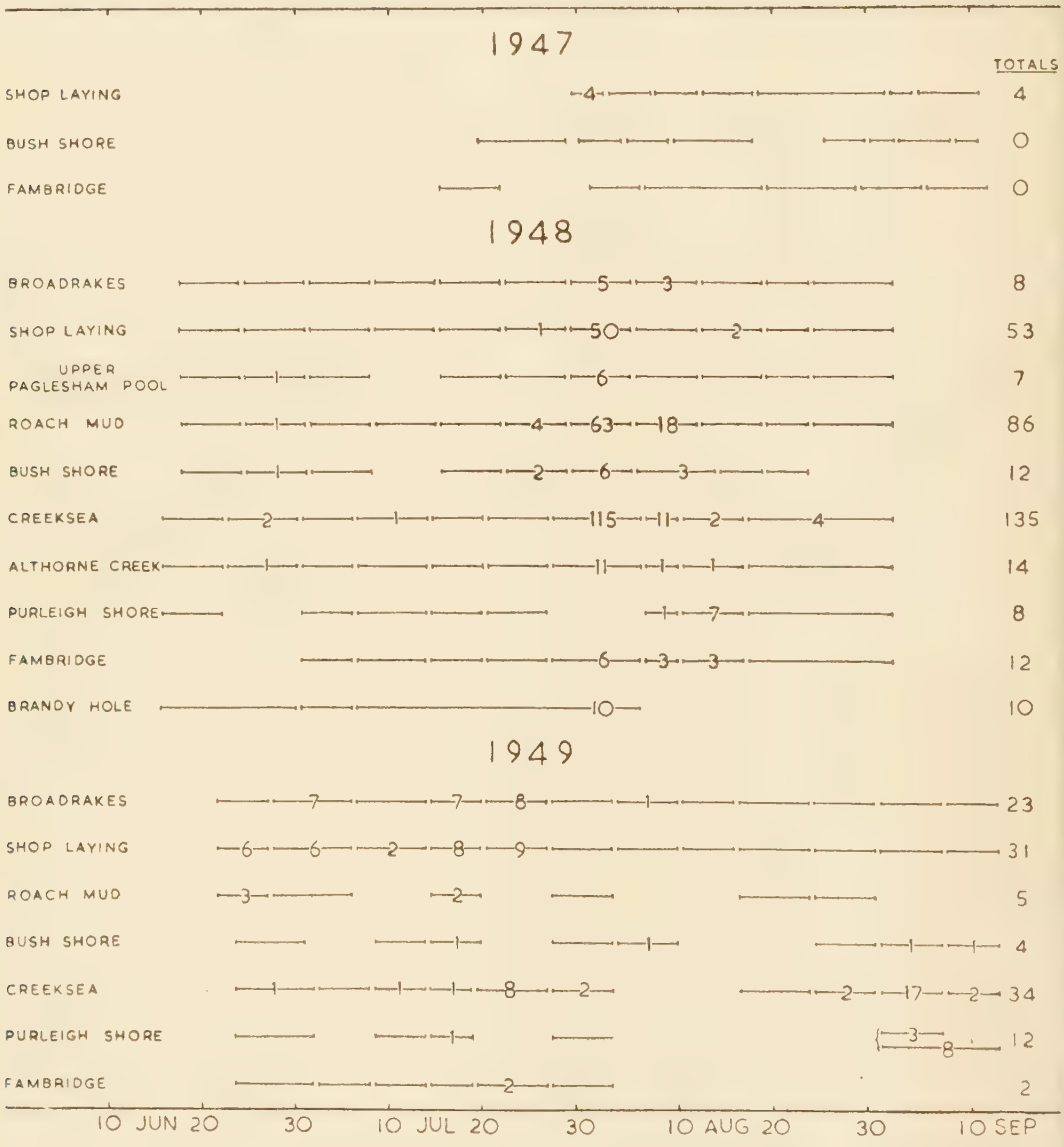


FIG. 8

Numbers of oysters spat recorded from slates at all stations. The periods of exposure of each sl (usually about 7 days) are indicated by horizontal lines. The positions of the stations are given in Fig. Most of the gaps in the records were due to losses of marker buoys.

The totals of spat counted on the slates from each area do not accurately indicate the distributi of the spatfall between the areas. Many spat settled on the slates exposed at the station " Roa Mud ", but no general spatfall occurred there, as the bottom was of bare mud. Oyster spat can settle abundantly in an area unless it contains plenty of surfaces suitable for attachment. T objects to which larvae most commonly attach themselves on Essex grounds are illustrated

Table 12, which is derived from the examination of a random sample of 401 oysters, 2 or 3 years old, dredged during May, 1947, in the R. Blackwater between Thurslet Creek and Shinglehead Point. The nature of the bottom over this wide area was varied and patchy. All the oysters were clearly attached to the objects on which they had originally settled. About half were attached, usually in clumps, to oyster shells, often to the shells of living oysters. Very many were attached to *Crepidula* chains, *Crepidula* being by far the most numerous member of the macrobenthos in Essex Creeks. These large chains usually bore only single oysters, being generally slimy and so unfavourable for attachment. Of the oysters attached to them, a third were attached to the inner surfaces of basal *Crepidula* shells, and only two-thirds to the very much wider areas afforded by the outer surfaces of the shells. Probably many had become attached soon after the occupants of the basal shells had died, for the inside surfaces of recently emptied shells are usually the only clean places on grounds infested with *Crepidula*. None were attached to single *Crepidula* shells, which are rare in most localities, for adult *Crepidula* usually live long and those which die automatically form the bases of newly-separated chains. Comparatively few oysters were attached to other shells or stones, which are sparse or of small size on most grounds, though not on all. On some grounds cockle shells are abundant, and many spat settle upon them (Mistakidis, 1951).

TABLE 12

Numbers of young oysters attached to naturally occurring objects in the River Blackwater, Essex, 1947

Objects which bore oysters	*Numbers attached to each object*	*Totals*
Outer surfaces valves of *Ostrea edulis.*	3, 2, 4, 4, 4, 2, 1, 6, 1, 8, 5, 11, 7, 6, 3, 4, 2, 1, 13, 1, 6, 1, 2, 1, 5, 2, 1, 1, 4, 2, 1, 1, 1, 1, 1.	118
Inner surfaces valves of *Ostrea edulis*	4, 1, 4, 1, 2, 3, 4, 1, 2	22
Both sides of *Ostrea edulis*	15, 12	27
Living *Ostrea edulis*	1, 2, 1, 6, 1, 5, 1, 2, 1, 1, 1, 1, 3, 3, 1	30
Outer surfaces *Crepidula* chains	3, 1, 2, 1, 1, 2, 1, 3, 1, 1, 1, 1, 1, 3, 3, 2, 1, 1, 2, 2, 2, 1, 1, 1, 1, 1, 1, 1, 2, 4, 1, 1, 1, 2, 3, 2, 1, 1, 1, 1, 2, 1, 1, 1, 1, 1, 1, 1

was still only about the average and Table 13 reveals no change in intensity of gregariousness from place to place. Probably the presence of very large numbers of densely laid oysters encourages setting up to a considerable distance. In other places between 2 and 22 spat per 10 shells were recorded from amongst the oysters and between 2 and 8 from the unstocked areas.

TABLE 13

Statistical analysis of evidence for gregariousness collected during 1948 (Table 4 in Knight-Jones, 1951a)

Source of variation in settlement density	Sum of squares	Degrees of freedom	Mean square	Variance ratio
Between localities	385·42	8	48·18	8·68
Between well-stocked and neighbouring unstocked grounds	37·83	1	37·83	6·81
Interaction localities x stocking	49·04	8	6·13	1·11
Between replicate shells	1716·34	310	5·54	1·00
TOTAL	2188·63	327		

The 1949 results gave further evidence of gregariousness. That Spring an additional 100,000 oysters had been laid on the lower half of the Shop Laying. Most of the spat observed occurred amongst these, amongst the other Brittany oysters, which had lain with little disturbance since the previous year, and on unstocked ground less than 100 metres away (Table 14). It is most unlikely that the heavy falls of spat on the Shop Laying during 1948 and 1949 were due to that ground being especially favourable for setting through some intrinsic quality, such as cleanness or exposure to currents. In 1947, when the ground was unstocked, the spatfall on it was negligible compared with that on the stocked areas at the mouth of Paglesham Pool, and it never appeared appreciably cleaner than other grounds sampled. By 1949 the stock on Bush Shore had also been built up considerably and a good spatfall occurred upon the shells there. Gregariousness seems an outstandingly important feature of the setting behaviour of oyster larvae. It provides a simple mechanism by which setting is concentrated on grounds which have proved suitable for the survival of the species.

TABLE 14

Survey of the spatfall on shells (of long-dead oysters) during 1949. Spat were most abundant near large stocks of oysters. The main spatfall at Fambridge and Purleigh Shore occurred long after this survey

Date and Locality:—	Approximate numbers of oysters laid within 100 metres	Oysters in dredge haul	Spat on sample of 10 shells from each haul: Numbers of spat on those shells which bore spat	Spat per 10 shells
4th July				
Upper Shop Laying	25,000	0	13, 6, 21, 13, 4, 8, 5, 17, 16	103
	75,000	52	30, 2, 14, 15, 13, 10, 2, 19, 3, 12	120
Lower Shop Laying	100,000	65	27, 21, 26, 4, 18, 12, 12, 12, 19, 3	154
400 metres below Paglesham Pool	0	0	2, 1, 1, 2, 2, 2, 1, 1, 6	18
Bush Shore ...	30,000	43	2, 10, 16, 9, 4, 5, 11, 1, 1, 4...	63
	0	4	2, 1, 2, 1, 1, 2, 1, 4	14
22nd July				
Broadrakes ...	10,000	8	2, 2, 2, 3, 3	12
	0	0	1, 2, 1, 1, 1	6
Common Shore	5,000	18	2, 4, 1, 1, 2, 1, 8	19
Upper Shop Laying	75,000	40	16, 7, 17, 8, 3, 17, 1, 2, 3	74
Lower Shop Laying	100,000	140	7, 5, 7, 12, 11, 7, 7, 9, 18, 11	94
Bush Shore ...	30,000	23	3, 11, 7, 10, 12, 7, 5, 6, 6, 1...	68
	0	3	2, 3, 4, 3, 8, 3, 2	25
23rd July				
Fambridge ...	10,000	58	1, 1	2
	0	0	—	0
Purleigh Shore...	10,000	20	—	0
	0	0	—	0

Figures derived from the examination of spat on old shells underestimate the inequalities of distribution which seem to be due principally to gregariousness, for a large proportion of the larvae setting on well stocked grounds attach themselves to the shells of living oysters, and still more to the shells of oysters which have recently died. The inside surfaces of recently emptied shells are much more favourable for attachment than the surfaces of old shells (Table 15). Since a similar predilection is shown for the inner surfaces of *Crepidula* shells, important causal factors are probably freedom from silt and orientation of surface. An examination of the distribution of spat on recently emptied shells (Table 16) showed that the inner surface of the cupped valve was especially favoured, probably because it usually presents an under surface, which larvae generally prefer (Cole and Knight-Jones, 1939; 1948; Knight-Jones, 1951*a*). The outsides of the flat valves bore fewest spat, probably because they usually lie against the substratum.

TABLE 15

Numbers of oyster spat on shells from three dredge hauls, September, 1948. A sample of recently emptied "clocks" (pairs of oyster valves) and another of old oyster shells were taken from each haul. All shells were free from mud and bore sessile organisms. All were searched so carefully that no oyster spat could have been overlooked. Most spat occurred on the inside surfaces of the clocks.

Place of haul	Number in sample of:		Numbers of spat on:		
	clocks	old shells	inside surfaces only of:		*both* surfaces of 10 old shells
			10 flat valves	10 concave valves	
Fambridge	10	11	21	43	10·9
Purleigh Shore ...	14	9	18·2	48·5	22·25
Creeksea	13	12	51·5	73	36·75

The 1949 survey of spat on shells showed practically no spat in the upper Crouch at Purleigh Shore and Fambridge, because it was carried out before the very late main spatfall had occurred there. It showed more spat on shells in the Roach than in 1948, probably because it followed the main Roach spatfall of the year more closely, for a heavy mortality occurs amongst spat during the first few weeks after setting (p. 37). The impression gained by subsequent examination of shells was that the Roach spatfall of 1949 was similar in magnitude to that of 1948. This is supported by the fact that similar numbers of eyed larvae appeared in the Roach during the two years (Table 10). The spatfall on slates was considerably heavier in 1948 than in 1949 (Fig. 8), but this was probably due in part to the fact that the main spatfall of 1948 was cataclysmic, occupying a short period during which there were very high concentrations of larvae in the eyed, swimming-crawling stage. When eyed larvae are sparse gregarious instincts prevent all but a few from setting on bare surfaces such as those of the slates, but when they are numerous heavy setting will follow attachment of a few. It was probably also due to the fact that the slates at some stations, such as Bush Shore, became crowded with the barnacle *Elminius modestus*, to an even greater extent in 1949 than in 1948, for it seems that such crowding discourages the attachment of oyster spat (p. 31).

TABLE 16

Distribution of oyster spat on recently emptied pairs of oyster valves ("clocks") from the Crouch and Roach, 1948.

Date	Number of "clocks" examined	Inner surfaces		Outer surfaces	
		cupped valve	flat valve	cupped valve	flat valve
July					
22	40	37	19	13	6
27	40	58	42	28	10
29	10	10	1	8	5
November					
3	26	66	22	19	16
Total	116	171	84	68	37

XI. SETTING OF THE BARNACLE *ELMINIUS MODESTUS*

It is not known when this Australian barnacle was introduced into Essex creeks. It wa recorded near Fambridge in 1945 (Crisp and Chipperfield, 1948), it was the most importan competitor of oyster spat for space on test slates during 1947 (Knight-Jones, 1948) and it set mor heavily in each subsequent year (Fig. 9).

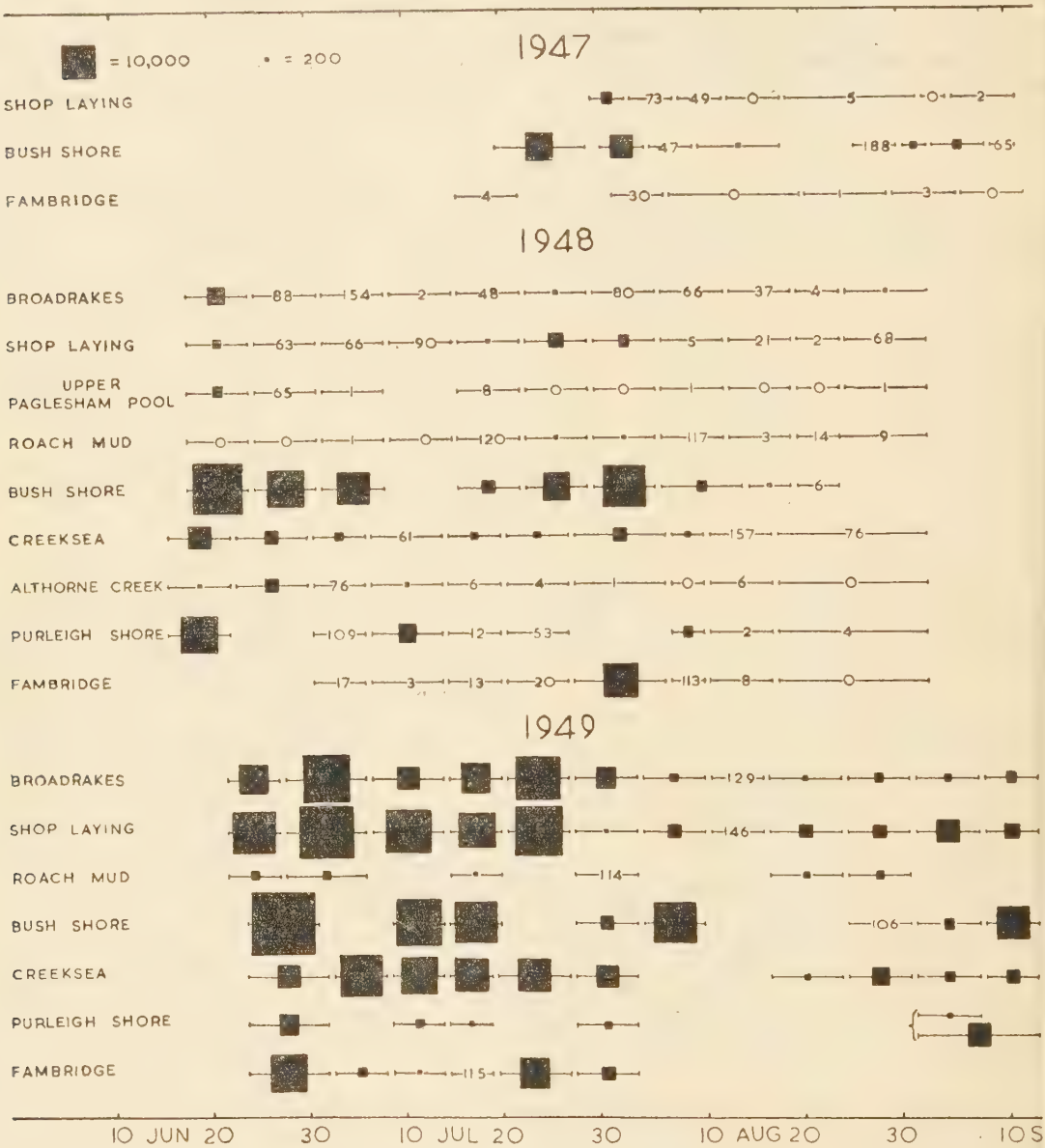


FIG. 9

As in Fig. 8, but showing the numbers of *Elminius* recorded from slates, indicated by the areas of bla squares, the smallest of which represents 200, the largest 37,500. Lesser numbers are given exactl There appeared to be an increase in each year. Setting was consistently sparse at stations where t bottom was of bare mud, such as Roach Mud and Upper Paglesham Pool. It was particularly heavy Bush Shore, where the slate was exposed on an area of clean shells which bore numerous adult *Elminius*.

Setting was at its peak in May and June, but continued quite heavily throughout the summe The results from slates during 1948 showed two peak periods of setting, an ill-defined one fro about 15th June to early July and a well-marked peak within the period 22nd July to 6th Augu setting between 15th and 22nd July being generally sparse. Oyster setting showed similar pea

ıt about the same times. It seems likely that the larval development of *Elminius* and of oysters vas held up by bad weather and shortage of nannoplankton in mid-July (Figs. 12 and 13), which suggests that larvae of *Elminius* compete with oyster larvae for the same food.

An oyster spat attaching itself amongst crowded *Elminius* must be at a disadvantage because of its small size and initially slow growth-rate, for a factor helping to determine which of two adjoining sessile organisms will grow over and smother the other, and so survive, must be the rate of advance of the growing fringe of each. When each adheres closely to the substratum, as in oysters and barnacles, the more rapidly advancing fringe may be expected to grow over the other. Measurements of the largest individuals on slates exposed at Creeksea from 31st August to 7th September and at Purleigh Shore from 31st August to 13th September, 1949, showed that oyster spat, with a dorso-ventral diameter of about 0·25 mm. at the time of setting, reached 1·7 mm. in a week (largest of 25 spat) and 1·9 mm. in two weeks (largest of 8); whereas *Elminius*, initially 0·5 mm. long, reached 1·0 mm. in a week (largest of 1,300) and 1·9 mm. in two weeks (largest of 4,970). On a slate exposed for 4½ weeks (2nd August to 4th September, 1947) the largest spat was 18 mm. and the largest *Elminius* 5 mm. Oyster spat grow mainly in a ventral direction, so the rate of advance of the growing margin is about the same as the increase in dorso-ventral diameter, whilst the almost stationary umbonal margin, being raised slightly above the substratum, is less likely to be overgrown by neighbouring organisms. Barnacles extend radially in all directions, so their increase in diameter must be halved to obtain the rate of advance of their growing margins. These considerations suggest that an oyster spat amongst crowded *Elminius*, which set a fortnight previously, will be in great danger of being smothered during its first week's growth, as the surrounding barnacles will be growing faster (Table 17). If it survives the first week it will be safer, for it will then be growing faster than the barnacles. Oyster spat which had settled more than a week previously were often observed to be growing over surrounding barnacles, but in the process they became misshapen.

TABLE 17

Comparison between approximate rates of growth of oyster spat and barnacles during the first few weeks after setting, from measurements given above. Oyster spat in their first week after setting do not grow as fast as barnacles in their third and fourth weeks, so would risk being smothered by setting on heavily barnacled surfaces.

Weeks after setting	Rate of advance (mm. per week) of the growing fringes of:	
	Ostrea edulis	*Elminius modestus*
to 1	0·45	0·25
to 2	1·2	0·45
to 4½	6·5	0·64

It appeared that oyster larvae did not expose themselves in large numbers to the dangers of setting on surfaces crowded with *Elminius*, for when shells exposed in wire bags on the Shop laying, during 1949, became covered with *Elminius* to varying degrees, it was found that few oyster spat settled on those which were completely covered (Table 18). Attachment to *Elminius* occurs comparatively rarely, perhaps because barnacles feed on oyster larvae (Cerruti, 1941).

On crowded surfaces *Elminius* were spaced out remarkably evenly. The most crowded slates were usually those from Bush Shore, about a mile below Burnham, where the weekly settlement per sq. cm. was rarely less than 10, usually lay between 20 and 40 and reached a peak of 90. Crowded individuals suffered a heavy mortality and did not grow well so that slates exposed for 4 weeks usually bore about 10 per sq. cm. of tightly-packed barnacles up to 5·5 mm. long. Shells on the bottom did not usually become so crowded. There was room for a fairly good oyster spatfall on shells at Bush Shore during 1949 (Table 14), whereas few spat settled on the slates exposed there (Fig. 8), which were very crowded with *Elminius* (Fig. 9). The rapid crowding of surfaces which are freshly exposed and raised off the bottom makes the use of artificial collectors for oyster spat rather difficult. If possible, collectors should not be sited on shelly shores, where setting of *Elminius* is particularly heavy, probably because of gregariousness (Knight-Jones and Stephenson, 1950). They should be put out on muddy shores, where there are no adult *Elminius*

and no solid surfaces on which cyprids can congregate through temporary fixation. The l time would be a few days before the main oyster spatfall. Though freshly immersed surfa are rather unfavourable for the attachment of oyster larvae (Cole and Knight-Jones, 1948:— see p. 35), very heavily barnacled surfaces are probably still more so.

TABLE 18

Oyster shells placed in wire bags at L.W.O.T. on the Shop Laying, on 22 June 1949, soon collected many *Elmi* A steady oyster spatfall was also in progress. On 14 July 53 of the shells were divided into four batches, which v covered to varying degrees by *Elminius*, and examined carefully. Numbers of oyster spat on the inside surface the shells in each batch are given below. No shell which was covered with *Elminius* bore more than a single spat. the shells which bore more than 4 spat were less than half covered.

Abundance of *Elminius*

(*a*) Sparse	(*b*) Shells less than half covered	(*c*) Shells more than half covered	(*d*) Shells entirely covered.
1	1	0	0
1	2	0	1
2	2	0	0
7	7	0	0
7	0	4	0
3	3	2	1
3	4	2	0
1	0	0	0
4	4	1	0
	1	2	1
	8	0	0
	5	0	0
	1	2	1
		3	0
		0	1
			0
Mean number of oyster spat per shell ... ... 3·22	2·92	1·07	0·31

XII. SETTING OF OTHER SESSILE ORGANISMS COMPETING WITH OYSTER SPAT

Total numbers of the most conspicuous organisms recorded from slates exposed for we periods are given in Table 19. *Balanus improvisus* is difficult to distinguish from the overwhelmi dominant *Elminius* within a week of setting, but slates immersed long enough to allow for gr to easily recognisable size were found to bear comparatively few *B. improvisus*. Thus four sl exposed at various stations during August 1947, collected 17 *B. improvisus* and 5,197 *Elmi* seven slates exposed from June to September, 1948, 23 *B. improvisus* and 20,267 *Elminius* sixteen glass plates exposed near Paglesham for most of August and September, 1949, 1 *B. impro* and 14,676 *Elminius*. The proportion of *B. improvisus* to *Elminius* therefore declined from a 1 : 305 in 1947, to 1 : 880 in 1948 and 1 : 15,000 in 1949. The ratios for 1948 and 1949 been applied to the numbers of barnacles recorded from the weekly exposures of each yea give estimated numbers of *B. improvisus* for Table 19. This species was setting more abund on shells below tide marks, where it was already well-established. It reaches a much larger than *Elminius* and is more difficult to remove when cleaning oysters for market, but as a compe of oyster spat on freshly immersed surfaces, such as those of slates and artificial collectors, it s comparatively unimportant.

Ostrea edulis was next in abundance to *Elminius*. Other molluscs were comparatively sp Although *Gryphaea angulata*, the Portuguese oyster, settled in considerable numbers on art collectors exposed above low water mark of spring tides at Paglesham during 1949, only on recorded from the slates, which were below low water mark, and only one eyed larva of this sp (Ranson, 1938) was observed in plankton samples. Spat of *Anomia* were not seen, these " oysters " being rather rare in Essex creeks, though constantly introduced on oysters imp from Brittany. Most of the post-larvae of other molluscs recorded in Table 19 were *Lit littorea* and *Cardium exiguum*. *Crepidula* often crawled on to the slates, but only a few indivi

TABLE 19

Numbers of various organisms recorded from upper/lower surfaces of test slates exposed for weekly periods at stations in the Roach and Crouch during the seasons 1948 and 1949

1948	*Elminius modestus*	*Balanus improvisus*	*Ostrea edulis*	*Crepidula fornicata*		Other post-larval Mollusca	*Dendrodoa grossularia*	Bryozoa	*Tubularia larynx*	Other Coelenterata
				post-larvae	older individuals					
Broadrakes	964/ 3,873	—	0/8	0/0	1/0	0/0	0/0	4/338	1/4	0/6
Shop Laying	4,198/ 2,767	—	14/39	0/0	4/0	0/0	58/19	0/10	0/0	4/11
Roach Mud	543/ 315	—	6/80	2/0	0/0	1/0	0/0	0/0	0/0	0/1
Bush Shore	51,350/45,800	—	8/4	2/0	1/0	0/0	0/0	0/0	0/0	4/4
Creeksea	5,216/ 6,230	—	33/102	2/0	6/4	0/0	0/0	0/0	8/1	0/2
Purleigh Shore ...	5,562/12,063	—	1/7	0/0	0/0	4/0	55/3	0/0	0/0	0/0
Fambridge	6,177/ 5,507	estimated	4/8	0/0	0/0	1/0	27/8	0/0	0/0	0/2
Totals	150,565	170	314	6	16	6	170	352	14	34
1949										
Broadrakes	30,428/41,098	—	11/12	0/0	0/0	2/0	0/0	0/19	0/0	24/7
Shop Laying	58,903/53,307	—	12/19	0/0	2/1	0/0	9/3	22/142	0/0	2/2
Roach Mud	1,782/ 1,390	—	3/2	0/0	0/0	1/1	0/0	0/0	0/0	0/0
Bush Shore	48,368/56,880	—	2/2	0/0	5/1	2/0	0/0	0/0	0/0	0/1
Creeksea	34,261/38,150	—	16/18	2/0	7/4	0/0	6/3	1/0	1/1	0/1
Purleigh Shore ...	3,222/ 7,822	—	0/9	0/0	0/0	2/1	16/7	1/4	0/0	0/0
Fambridge	12,508/10,664	estimated	2/0	0/0	0/0	4/1	37/9	0/6	0/0	0/0
Totals	398,783	27	108	2	20	14	90	195	2	37

small enough to be regarded as recently settled post-larvae were observed. These measure 0·86 mm. in length, and appeared only after periods when growth of oyster larvae had been takin place (Fig. 10), suggesting that larval growth of *Crepidula* and of oysters was limited by simila factors. Most appeared at Creeksea, where adult *Crepidula* were particularly numerous, whic supports a view expressed to me by Mr. P. R. Walne, that *Crepidula* larvae are gregarious durin settlement.

Dendrodoa grossularia was often found on slates from the Shop Laying and from nea Fambridge, where adult *Dendrodoa* are abundant. Its short pelagic life will largely account fo this localised distribution (Fig. 10). It is rather unimportant as a competitor of oysters, excep where present in great abundance, because of its slow growth and small size.

Ascidiella aspersa is a serious pest in certain creeks off the River Blackwater, where its abundanc on neglected grounds leads to oysters being smothered in mud, but it is comparatively scarce i the Crouch and Roach.

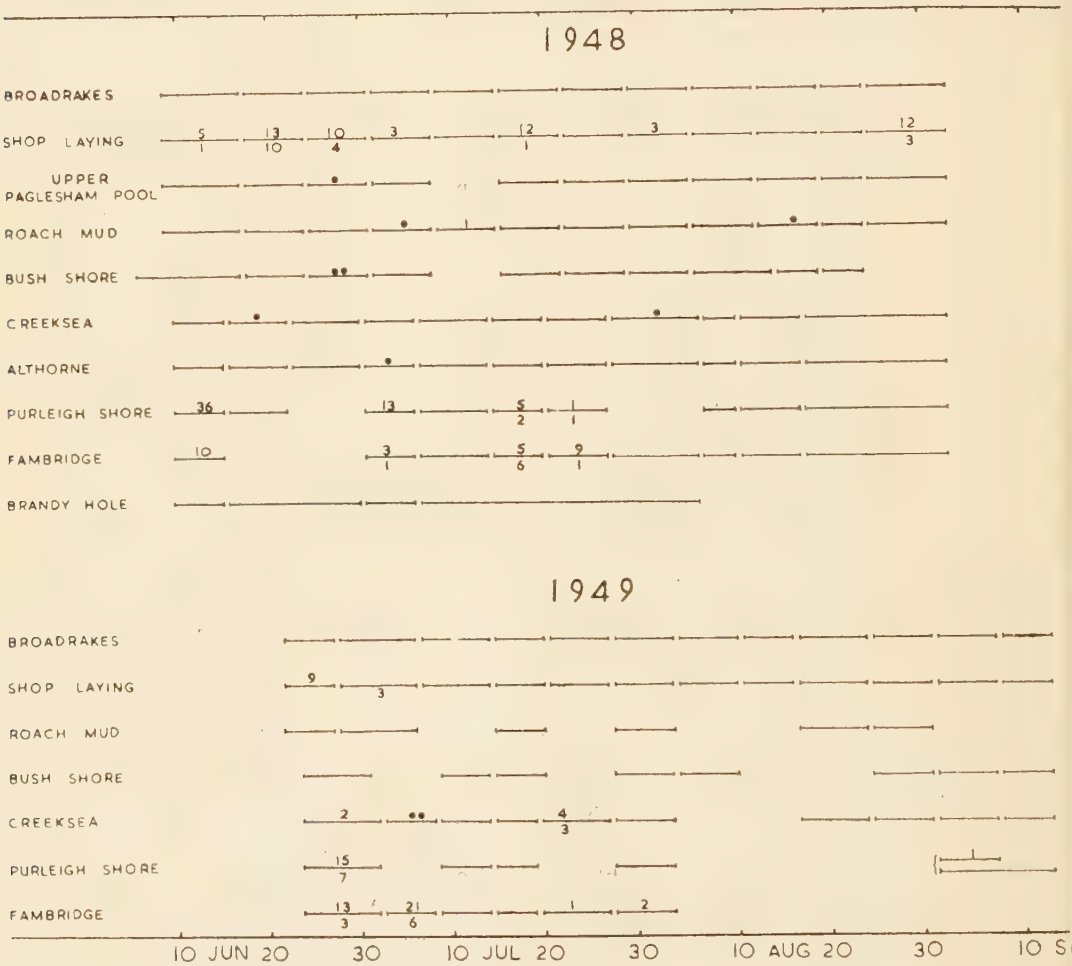


FIG. 10

As in Fig. 8, but showing numbers of *Dendrodoa grossularia* setting during 1948 and 1949, as an exam of a species showing a localised distribution. The figures above and below the lines represent the numb on the upper and lower surfaces respectively. Fewer appeared during 1949, perhaps because the sl were so crowded with *Elminius*. The black spots represent *Crepidula* post-larvae. The times at wh these appeared (late June and early August, 1948; early July, 1949) were also favourable for set of oysters.

Osburn (1944) has rightly pointed out that encrusting Bryozoa are often serious pests on oy beds, since oyster larvae cannot settle on their extensive colonies. The only encrusting fo abundant at Burnham was *Membranipora*. Examination of artificial collectors in 1948 indica

that hundreds of spat had been smothered by *Membranipora lacroixii*. Shells were commonly covered with a thin film of this form, and several spat were observed in the process of being sealed down by its rapidly spreading growth. Being dingy and inconspicuous it is not usually noticed by oystermen. Probably the cyphonautes larvae of *Membranipora* are gregarious during setting, for examination of four similar slates, which had been exposed side by side at the station Roach Mud from 1st to 8th July, revealed 92 *Membranipora* colonies on the underside of one slate, none on its upper side and none on any of the other slates. Only one *Membranipora* colony was observed during the routine counts of slates exposed for weekly periods. The other Bryozoa recorded were erect forms, including *Bugula flabellata*, *Scrupocellaria scruposa* and *Bicellaria ciliata*, which appeared to be harmless to oysters.

Tubularia larynx occurred infrequently on slates, but became very abundant on bags of shells, which were suspended from a pontoon fouled with its breeding colonies. It may well have reduced the spatfall on these shells by feeding on oyster larvae. Other hydroids, actinians, ostracods, copepods and Foraminifera were occasionally recorded from slates, whilst small, delicate mud tubes, probably of post-larval polychaetes and amphipods, were common amongst sediment on the upper surfaces.

Certain species were found preponderantly either on upper or lower surfaces (Table 19) Oyster spat were commonest on lower surfaces, unless the slates were thickly covered with *Elminius*, when the oysters setting showed less discrimination (Knight-Jones, 1951*a*). Bryozoa were much commoner on lower surfaces, but *Dendrodoa* and post-larvae of *Crepidula* and other molluscs were commoner on upper surfaces.

XIII. USE OF ARTIFICIAL COLLECTORS FOR SPAT

Wire bags containing shells have been used as spat-collectors in America, placed in heaps on ground too muddy for the laying of loose shells. Bags of about 200 shells laid on the ground just below tide marks at Common Shore, in the Roach, during the summer of 1948, were found at the end of September to contain only about 30 spat per bag. Some of the bags had contained a few young oysters in addition to the shells, but these did not catch consistently more spat than bags containing shells only. The bags became smothered with silt to varying degrees and this appeared to have been unfavourable for the attachment of spat. Similar bags, which were suspended from a float at a depth of a metre over the Shop Laying, became smothered with *Tubularia larynx*, but contained about 50 spat per bag at the end of September. Immediately before the main spatfall of 1948 two sets of three bags were put out at low water of spring tides on Bush Shore, one set containing shells which had just been dredged from below tide marks, the other bleached shells which had lain for years on saltings above mean high water mark. It was expected that the dredged shells would collect more spat than the bleached shells, since experiments in the Conway tanks had shown shells fouled with sessile organisms to be more favourable for attachment than clean shells, but when the shells were examined on 27th September considerably more spat were found on the shells which had been bleached (Table 20). This experiment was not strictly comparable with those at Conway, and the different result may have been due to differential mortality amongst settled spat, or to the silt of an estuarine environment, but it suggests that the practice of laying bleached cultch on an oyster bed, immediately before a spatfall, is a sound one. The yield of spat from shells in bags was no better than from shells lying on good oyster grounds.

TABLE 20

Numbers of spat recorded from bags of shells exposed during August and September, 1948. One set of bags had been filled with dredged shells, which bore living organisms, the other with bare sun-bleached shells. Bags which became particularly muddy are marked (*).

Size of bags (and numbers of shells contained)	Dredged shells	Bleached shells
Small (200–250)	22	79
Small (200–250)	16	21(*)
Large (350–400)	29(*)	62(*)
Totals	67	162

The very productive French oyster industry is based on the use of limed tiles to collect spa (Dalido, 1948). Several hundred large ridging tiles, each about half a metre long, which wer stacked on saltings near Burnham and which bore traces of lime and shells of marine organism indicating past use as experimental spat-collectors, were kindly given to us by the landowne Mr. Alec Steel. Several hundred smaller tiles, of the type which the French tie together to mak " bouquets " (Cole, 1938*b*), were kindly lent to us by the Seasalter and Ham Oyster Fisher Company. These also had been used in past experiments. All the tiles were limed on 12 Ma 1948.

On 21st June about two hundred of the large tiles were planted out at low water of sprin tides on the Shop Laying, Paglesham. They were stacked about eight deep on a firm botto of shells and mud, surrounded by sticks stuck vertically into the mud, and tied down by wir passing over the top layer of tiles. A similar batch was planted out on 9th July at low water average tides. The main spatfall occurred at the beginning of August and the spat on ten til from each batch were counted on 20th October. The average number per tile was 27 from th batch which had been planted out earliest and 34 from the other, but the spat were too small remove. In November the tiles were taken up and stored in an oyster pit, to avoid the attacks *Urosalpinx* and reduce the danger of frost damage. In April a further sample of tiles w examined, one of which bore 18 spat, many 5, some none; the average was 3 or 4 per tile of sp nearly large enough to be removed.

These single tiles proved to be more awkward to handle than the larger collecting units dea with below. The method of stacking on the bottom allowed invasion by *Urosalpinx*, which destroy many spat, whilst the tiles forming the bottom layer became smothered with silt and so caug no spat.

The French tiles were wired together to form about forty bouquets, each of ten tiles. The were planted out between 9th June and 9th July at low water of spring tides at various places. Th were suspended clear of the bottom from sticks, each of which was planted deeply in the mud a passed vertically through the middle of a bouquet. On 4th, 5th and 6th September eleven bouqu bore numbers of spat varying from 50 to 360 per bouquet (Table 21). The bouquets were kept an oyster pit during the winter and unwired for scraping on 27th April, when over three hundr of the poorest tiles yielded 1,162 spat, which were mostly very small. Sixty tiles remaining, whi each bore at least 10 spat, were not scraped, but were re-wired and put out again at low water allow further growth. In July about 1,500 fair-sized spat were removed from them. The yi from bouquets may be estimated as little more than 5 one year old spat per tile.

Egg-box collectors were also prepared, as used in Canada and Australia (Needler, 19 Kesteven, 1941). Dr. S. M. Marshall and Dr. R. B. Pike kindly gave advice on their constructi The small cubical type with sides about 30 cm. long, made of four egg-box partitions side by si enclosed in wire netting, seemed easiest to handle. The collectors were wired first, wetted, dipp in a suspension of fine sand, cement and slaked lime in equal parts, allowed to harden and th dipped again. In 1948 twenty-five were prepared and planted out beside the bouquets. So were placed on the ground, but this allowed invasion by *Urosalpinx*. Others were suspended wire from fairly thick sticks planted vertically in the mud. Each stick bore four collectors, attach by their corners and orientated so as to present a minimum of vertical surfaces, since these unfavourable for the attachment of oyster larvae. In November all were stored in an oyster and in April some were put out again at low water. In July all were broken up, about 150 fair-si spat being obtained from each.

The spatfall on collectors at different localities was assessed by examining bouquets a mo after the main spatfall of 1948. Those from the Roach bore on an average about twice many spat as those from the Crouch. Table 21 gives number of spat from each bouquet, fr other artificial surfaces nearby (i.e. the test slates and the concrete blocks which held them) from samples of shells from the surrounding ground. Although much the heaviest spatfall shells occurred amongst the very large stock of oysters on the Shop Laying, the spatfall on artifi surfaces exposed there was not remarkably heavy. As in Holland (Korringa, 1950) there see no advantage to be gained by placing collectors near large stocks of oysters, probably beca larvae settle amongst the oysters rather than on the collectors. Particularly large numbers larvae attached themselves to artificial surfaces exposed at the station Roach Mud, where th were no oysters, perhaps because there was nothing else suitable for attachment there.

TABLE 21

Numbers of oyster spat recorded at various stations during 1948 from naturally-occurring surfaces (i.e., old oyster shells and the inside surfaces of recently emptied pairs of oyster valves) and from artificial surfaces. The stations are arranged in order of proximity to oyster stocks, to show that though the spatfall on shells was generally heaviest amongst or near to the largest stocks, the spatfall on artificial surfaces showed no sign of such a correlation. A dash indicates no observation.

	Natural surfaces			Artificial surfaces			
	10 pairs of valves from well stocked areas	10 old oyster shells from areas which were:—		test slates exposed for:—		upper surface (ca. 35 × 65 cm.) of concrete block	"bouquet" of 10 tiles
		well stocked	un-stocked	whole season	weekly periods		
Shop Laying	259	51·1	28	6	53	20	177
Common Shore	29	14·5	7·5	—	—	—	364
Broadrakes	64	6·3	7·1	2	8	19	100
Lower Paglesham Pool... ...	—	—	—	—	—	—	149
Creeksea	125	5	3	8	135	66	—
Purleigh Shore, well stocked area	66	8	—	8	8	45	158
Fambridge, well stocked area ...	64	2	—	4	12	14	52
Purleigh Shore, unstocked area	—	—	2	—	—	—	95
Fambridge, unstocked area ...	—	—	3·5	—	—	—	85
Althorne Creek Mouth... ...	—	—	—	10	14	34	93
Upper Paglesham Pool... ...	Nil —	bare mud	—	0	7	—	152
Roach Mud	Nil —	bare mud	—	—	86	239	293

The lower surfaces of many tiles were smothered with *Membranipora* (p. 35) and these bore no spat. Competition for space amongst sessile organisms was keenest on lower surfaces and most spat occurred on the upper surfaces of the tiles.

It is probably best to plant collectors on bare muddy ground, to delay colonisation by barnacles (p. 31). In 1949 tiles and egg-box collectors were planted out on muddy ground adjoining the Shop Laying, but all were covered with barnacles almost immediately, since *Elminius* was particularly abundant and the collectors were perhaps not far enough from patches of shell, where the cyprid larvae of barnacles congregate. The oyster spatfall upon them seemed similar to that of 1948. Many of the egg-box collectors were broken prematurely by wave action, as they had been given only a single dipping in the concrete mixture, which produced too thin a coating. On 15th December two of the egg-box collectors, which were damaged and incomplete, were broken up, yielding respectively 176 and 260 spat. Twenty tiles which were examined bore an average of 12 spat per tile, many large enough for *detroquage*, but a remarkably high proportion (about 20 per cent) were *Gryphaea angulata*. There was no opportunity to assess this season's yield of one year old spat.

Further experience in the handling of artificial collectors is needed before judging their commercial possibilities in Essex. Certainly the cost of handling and of buying tiles, or making egg-box collectors, would be high. It may roughly be estimated that each egg-box collector costs 1s. and may be expected to yield 100 one year old spat (2s. per 100 in 1949) provided the season is not much less favourable than 1948 or 1949. It is unlikely that such a return would cover the cost of handling and attention, and the risks of spatfall failure, winter losses, or market flooding by brood oysters from other sources.

XIV. LOSSES AMONGST SETTLED SPAT

Immediately after the sparse spatfall of 1947 several spat were found on shells in the Crouch, but none could be found a few weeks later, which suggested that there had been a considerable mortality soon after setting. Examination of tiles on the Shop Laying after the main spatfall of 1948 indicated that the mortality amongst spat had been very high (perhaps over 90 per cent) during the first month after setting, about 50 per cent during the second month and over 50 per cent during the following winter (Table 22). Counts of spat on shells also indicated that the mortality was high during the first month and about 50 per cent during the second. The mortality amongst three and four year old oysters seemed to be only about 20 per cent per annum.

TABLE 22

Numbers of spat on lower surfaces of limed tiles at varying periods after the spatfall, which occurred about 1st August, 1948

11th August (single tile)	295 per tile
5th September (average of 4 tiles)	15 per tile
20th October (average of 11 tiles)	7 per tile
27th April (estimated, after examination of 50)	2 per tile

Recently settled spat are exposed to many dangers, prominent amongst which are attacks b *Urosalpinx* and *Carcinus*, and smothering by silt and sessile organisms. Fully grown *Urosalpir* and *Carcinus* eat quite large spat. Cole (1942) has shown how recently hatched *Urosalpin* which are inconspicuous but occur in great numbers, feed on recently settled spat. New metamorphosed *Carcinus*, which are also abundant during August and September, are of a si suitable for feeding on the smallest oyster spat. Spat can survive smothering by silt to a remarkab degree, but many were observed to have been killed by it.

In 1949 great numbers of one year old oysters were collected from the upper reaches of tl Crouch and Blackwater. The upper reaches of Essex creeks generally yield particularly lar numbers of young oysters. This abundant production is due to the presence of wide areas shelly or stony bottom, kept clean by the movement of shallow tidal waters and the absence many sessile animals which encourage silt-deposition in the lower reaches. *Crepidula*, for instanc was almost absent from the upper Crouch during the period under review, having suffered 100 per cent mortality there during the severe weather early in 1947. Clean shells favour t attachment of oyster spat and lack of silting and of variety in the fauna favour their subseque survival. *Urosalpinx* was not to be found in the upper Crouch and probably unrecognis predators of the lower reaches were also absent. To judge from examination of shells and te slates and the distribution of eyed larvae the density of the 1948 spatfall was no greater in t upper reaches than lower down. The large yield of one year old oysters in 1949 seems to ha been principally due to a high rate of spat-survival in the upper reaches during the mild wint The removal of young oysters from such nursery grounds to grounds lower down, where they a safer from the effects of unfavourable winter weather, is established practice amongst Ess oystermen.

XV. SUMMARY OF EVENTS DURING THE THREE SEASONS

1947

The water temperature of the Crouch must have been about −2° during most of the six wee of severe weather which ended on 4th March, for ice floes abounded. The Spring was genera fine and May was so hot that towards the end of the month water temperatures exceeded 20° the Blackwater, and so probably in the Crouch too, but on 5th June the weather broke a remained cold or changeable for over a month.

Sampling at Burnham began on 9th July. A few oyster spat had already appeared Paglesham Pool, their size suggesting that they had settled about 6th July. Planktonic lar were usually less than 30 per 100 litres, the weather was rough, the water temperature was bel 18°, nannoplankton flagellates were sparse and very few larvae showed any growth. From 12th J until September the weather was extraordinarily fine. As the water temperature rose above 2 the density of flagellates increased and large larvae appeared in the samples, but numbers of lar remained low (Fig. 11). At the end of July there was a spatfall, which appeared heavier than earlier one, but which was nevertheless very light. Thereafter few larvae were liberated a practically no large larvae were observed, though conditions appeared very favourable, with wa temperatures exceeding 20° throughout August.

The poor production of spat during this season may largely be accounted for by parent sto being very small and in poor condition after the severe winter. Essex oystermen believe t spatfall failures usually follow severe winters (Laver, 1916).

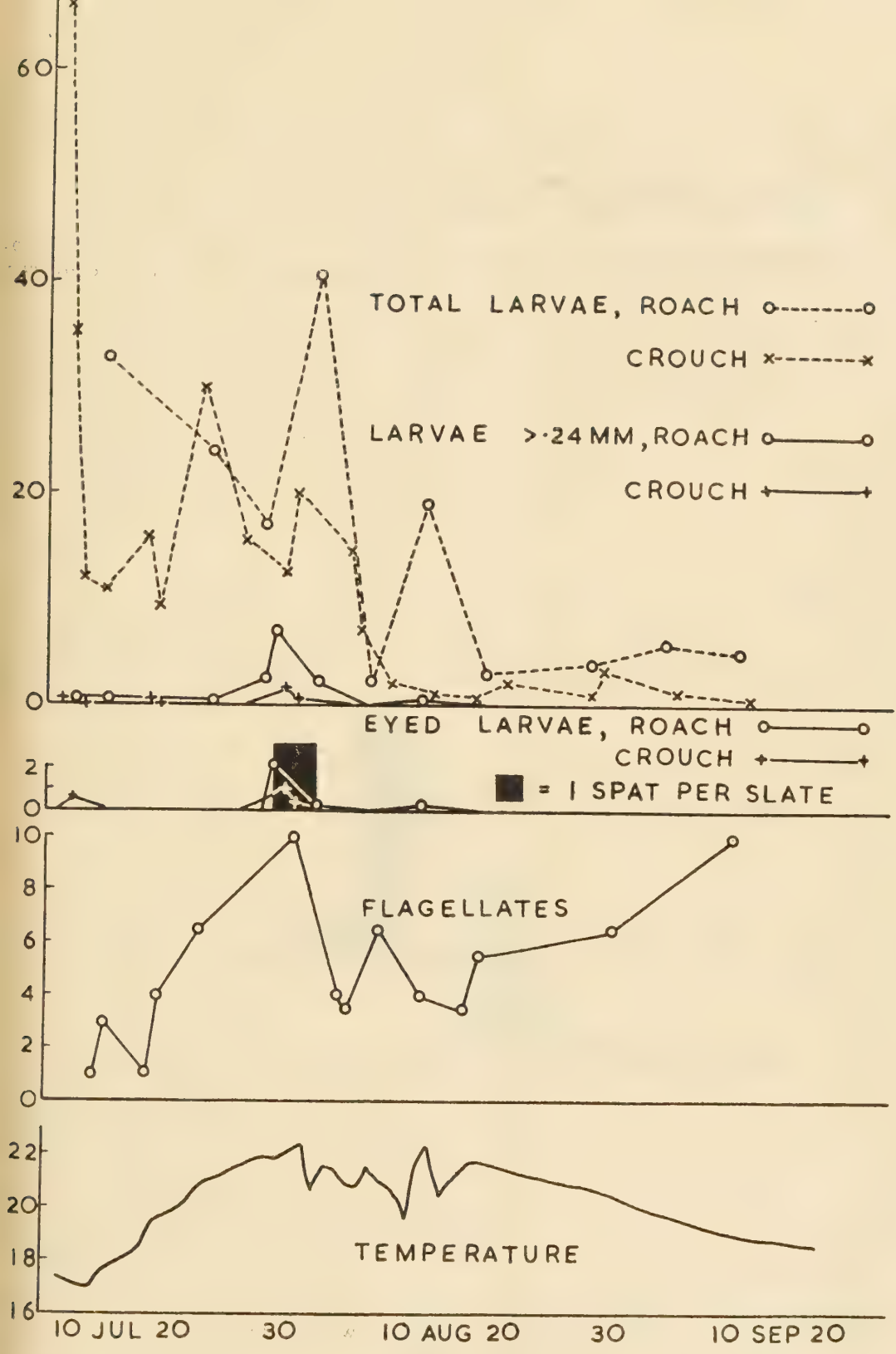


FIG. 11

he main period of larval growth during 1947, illustrated by fluctuations in numbers per 100 l. of larger rvae, correlated with numbers of larvae of all sizes, numbers per cubic mm. of nannoplankton flagellates a size (2–10μ) suitable for food, and water temperatures. All the nannoplankton samples and water mperatures were taken at Burnham. Numbers of non-motile algae are not included. The spatfall on st slates is shown as a histogram, the area of which represents the numbers of spat recorded, its horizontal extent the period of exposure. There was no spatfall on two slates exposed in the Crouch.

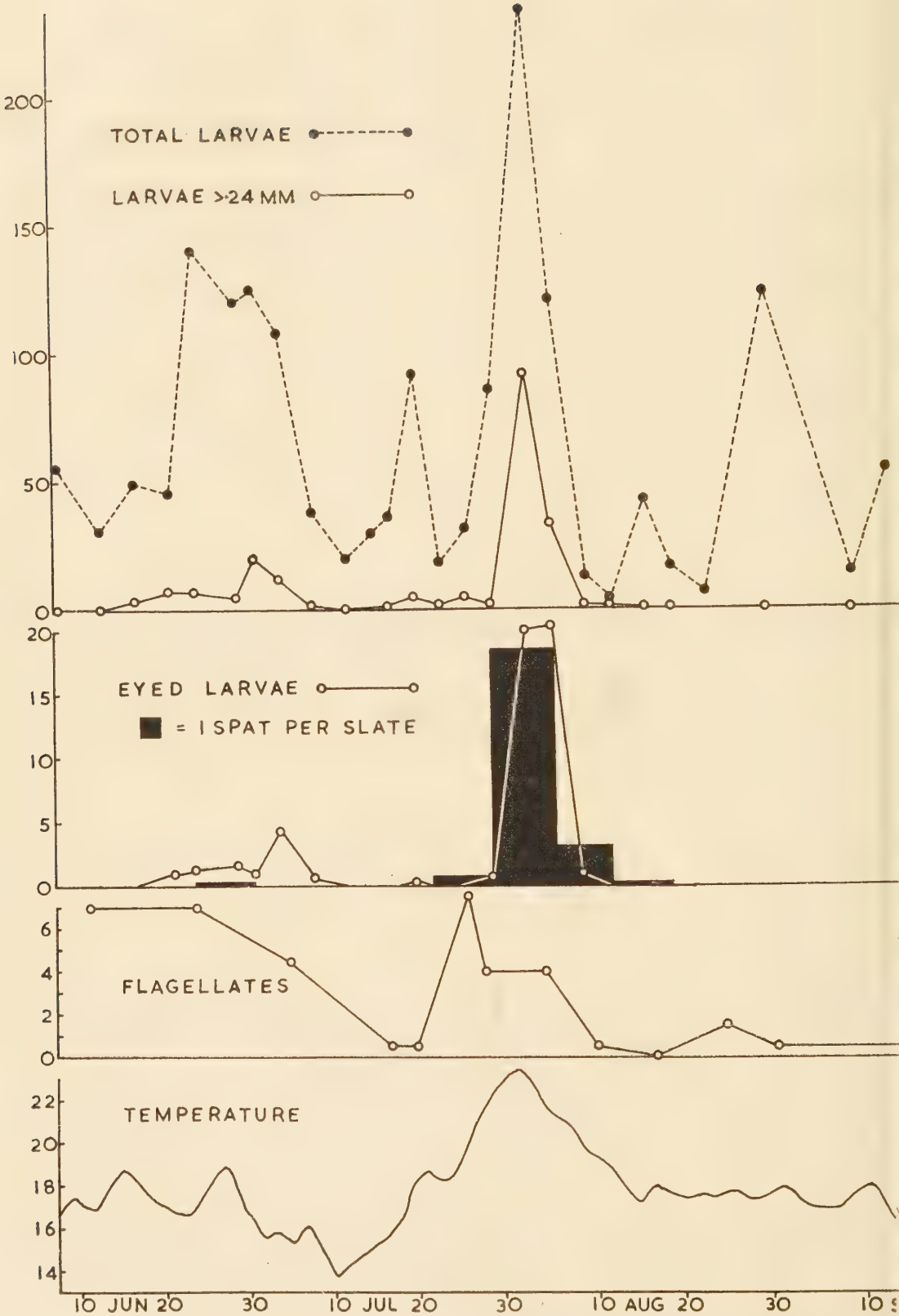


FIG. 12

Periods of larval growth in the Roach during 1948, illustrated as in Fig. 11. Records of flagellates from the Roach and lower Crouch, temperature records from Paglesham Reach.

948

The following winter was mild but the weather during the summer of 1948 was generally cold nd rough. Stocks of parent oysters were not much greater than in 1947, but were probably in uch better condition. Oyster larvae were recorded from early June until early September. They ere about twice as numerous as in 1947. In low water samples from the lower reaches of the oach, there were often 100 and occasionally 300 larvae per 100 l.

The weather in June was changeable and water temperatures did not exceed 19°, but annoplankton flagellates were about 5 per mm.^{3} and large larvae were common, producing a small patfall about the end of the month (Figs. 12 and 13). The first half of July was cold and rough. lagellates became sparse, large larvae almost disappeared from the samples, and settlement of *Elminius* became less heavy (p. 30). The latter half of July was very hot, especially during the ast week of the month. Flagellates were again about 5 per mm.^{3}, water temperatures rose steeply o more than 22° and larvae showed exceptionally good growth and survival (p. 22). The spatfall hich followed was intense but short-lived. A period of colder, dull weather began on 2nd August, umbers of larvae and flagellates fell sharply and no more growth of larvae was observed.

In this season the production of spat, though only moderate, was much greater than in 1947. o judge from the numbers of eyed larvae recorded, it was about ten times as great (Table 10).

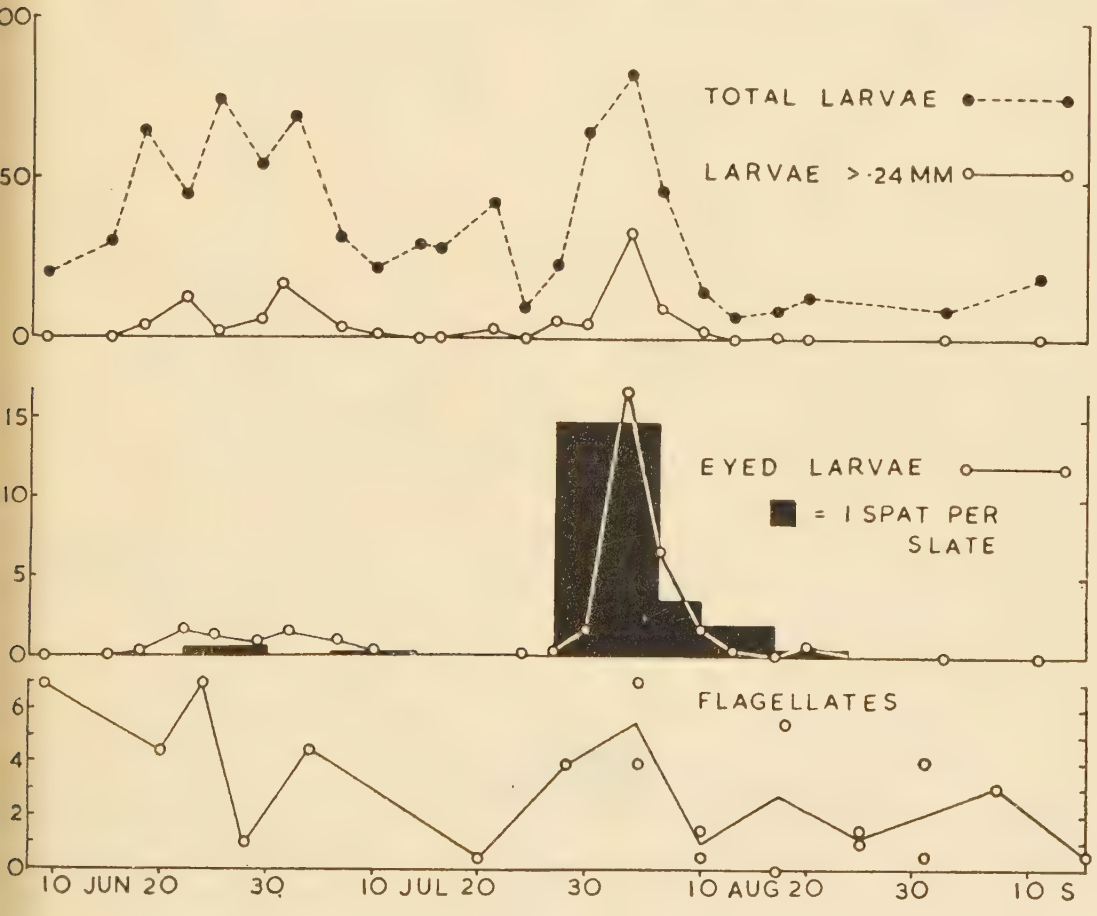


FIG. 13

eriods of larval growth in the Crouch during 1948, illustrated as in Fig. 11, but without giving the mperature fluctuations which were similar to those in the Roach (Fig. 12). Records of flagellates are from the Crouch.

949

The winter was again mild and the summer was warm and exceptionally dry. Parent stocks ere somewhat larger (p. 24). Larvae were recorded from early June to early September. Con-ntrations of larvae in the Crouch were similar to those of 1948, but those in the Roach were

about twice as great, often exceeding 200, and once (on 21st June) reaching 877 per 100 l. T
varied size and distribution of the larvae in this last sample showed that they were not deriv
from a local liberation. The weather in the second half of June was favourable, the wa
temperature soon exceeded 19° and fairly good growth of larvae occurred in the Roach. A
unusually early spatfall began on 20th June and continued at a moderate or low intensity ur
late in July (Fig. 14). The spatfall in the Crouch during this period was slight because numbe
of larvae there were very low. Later few spat settled in the Roach, but concentrations of larv
in the Crouch increased during late August and a moderate spatfall occurred there at the beginni

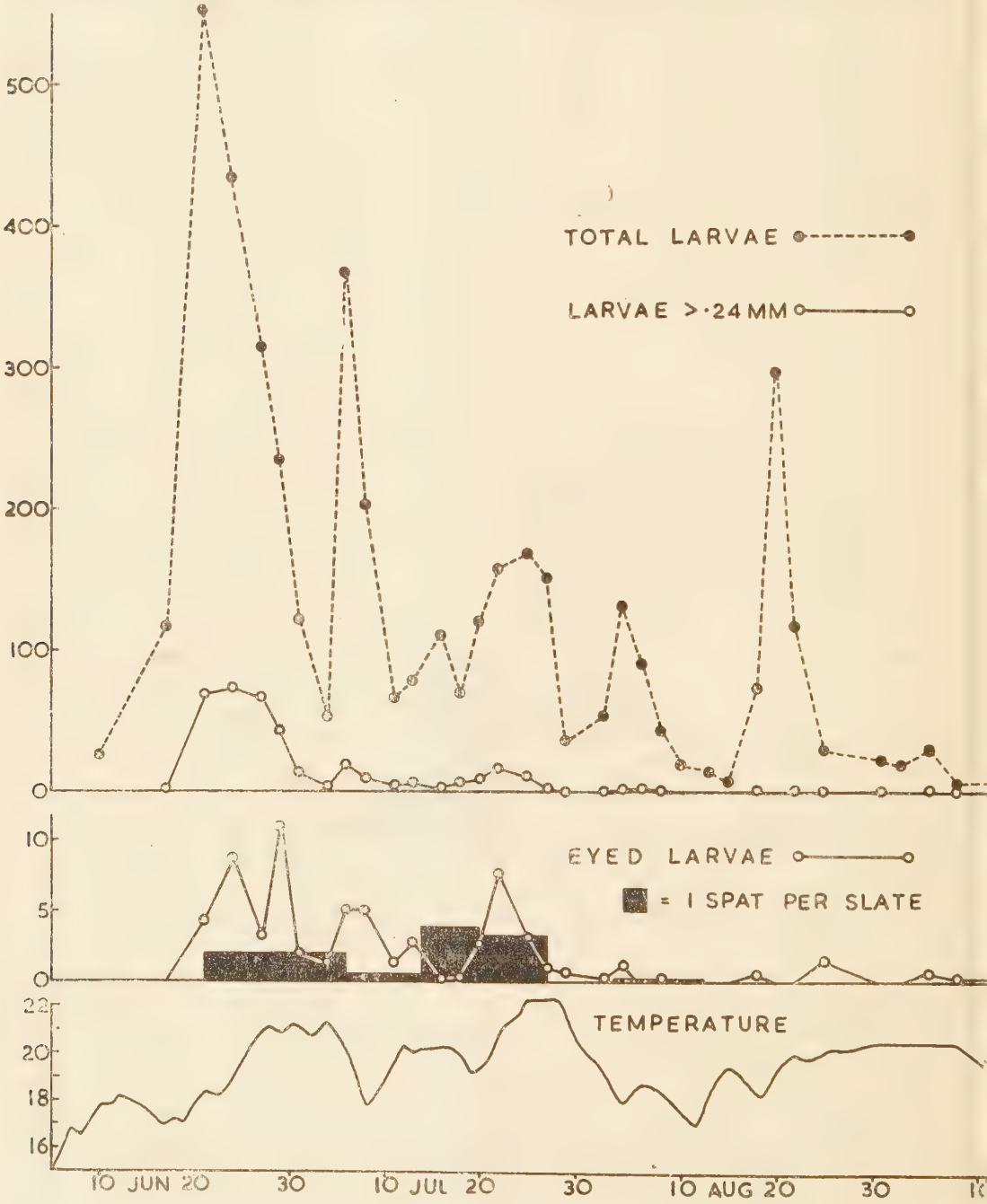


FIG. 14

Periods of larval growth in the Roach during 1949, illustrated as in Fig. 11, but without records of flagellates (p. 9). Temperature records are from Paglesham Reach.

of September (Fig. 15). This followed very good growth and survival of larvae during a period when the weather was particularly fine and nannoplankton flagellates were about 5 per mm^3.

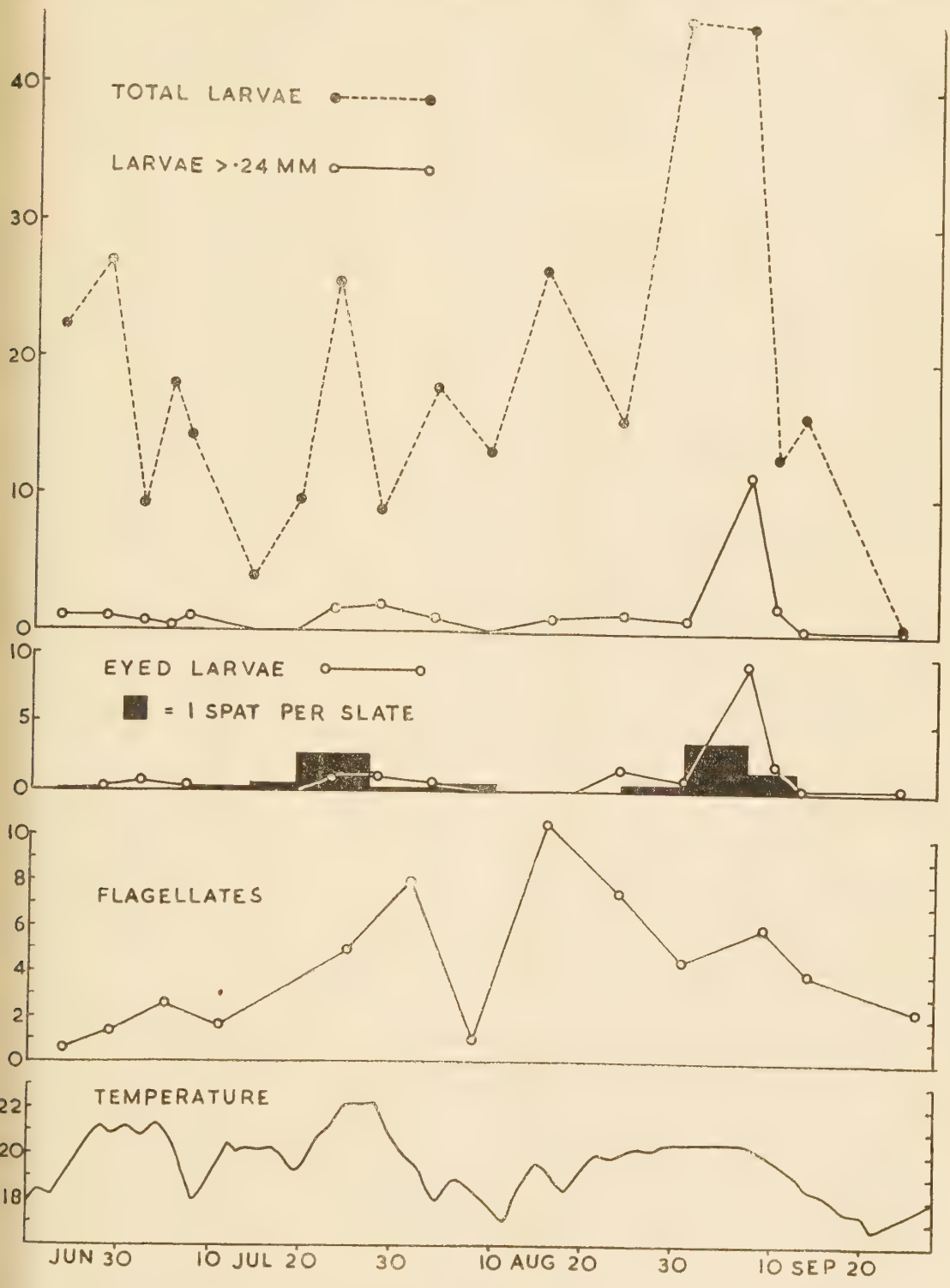


Fig. 15

eriods of larval growth in the Crouch during 1949, illustrated as in Fig. 11. Records of flagellates are from Burnham at low water; temperature records are from Paglesham Reach.

Although the weather and the course of events in 1949 were very different from 1948, th production of spat was similar, to judge from the numbers of eyed larvae recorded (Table 1 and from spatfall on shells. More spat was recorded from test slates during 1948, but this w probably because the 1948 spatfall was so intense over a short period (p. 29). The 1949 spatf in the Roach was of greater value than that of 1948, being earlier, whereas that in the Crou was of somewhat less value, being mainly late. Water temperatures remained generally muc higher than in 1948, but the warmest period (at the end of July) was not quite so warm as th same period of 1948, when the peculiarly intense spatfall occurred.

XVI. A DISCUSSION OF THE FACTORS AFFECTING SPAT PRODUCTION

The numbers of larvae produced in a season may be expected to depend largely on the si of the parent stock. Korringa (1947) demonstrated this relationship in the Oosterschelde. 1947 parent stocks near Burnham were obviously very sparse, but by 1949 it seemed that tho in the Roach were already approaching an adequate level. Concentrations of larvae in the Roa then were of the same order as those recorded by Korringa (1941): they could have produc a heavy spatfall if a large proportion had grown to settlement size, but comparatively few did s As expected, the stage when the larvae first find themselves free from the parent, seeking the own food, proved to be critical. Rates of growth and survival fluctuated greatly and were usua negligible (p. 22). Rapid growth and high percentage survival, at the end of July, 1948, produc in a few days about as many spat as settled in all the remainder of the three years.

Heavy losses of oyster larvae are usually regarded as being due to predators and to dispers by currents (Korringa, 1941). Cerruti (1941) compiled a formidable list of animals which found feeding on oyster larvae. At Burnham comparatively few larvae are swept out to sea (p. but many must be consumed by vast stable populations of filter feeders, such as *Crepidula*, barnac and ascidians, and ephemeral swarms of such animals as *Aurelia*, *Pleurobrachia*, small fishes a perhaps even *Noctiluca* (Dodgson, 1922). Korringa (1941) explained the apparent anoma that cold weather seems unfavourable to survival of larvae though they are not killed by l temperatures in the laboratory, as being due to slow development at lower temperatur allowing an increased toll to be taken during the planktonic stage. The substantial eleme of truth in this idea can hardly be doubted. Large larvae were never seen at Burnham in a numbers unless the temperature was about 19° or higher. Best survival followed a rise temperature to over 22°. Loosanoff (1951) showed that the development of lamellibranch larv is prolonged by low temperatures alone, in experiments where food was abundant. Unc natural conditions the bad weather which causes a fall in water temperature is also follow by scarcity of nannoplankton (p. 9), and Loosanoff (1950) has stressed the importance to oys larvae of enemies and food. Imai and his associates (1951) found that growth and settlem of oyster larvae in Mangoku-Ura inlet occurred at a season when the flagellate population increas from a basic level of about 1 per $mm.^3$ to about 5 per $mm.^3$ Similar increases were genera observed at periods favourable to growth of oyster larvae at Burnham.

Since fluctuations in abundance of food and predators are complicating factors, it is diffic or impossible to fix a lower limit of temperature below which larvae development will not completed under natural conditions. During most of 1949, when the temperature remain between 19° and 21°, rates of growth and survival appeared to be lower than at the end of Ju 1948, when temperatures had reached only 17° to 19°. It seemed that sustained high temperatu were not as favourable to larval development as marked improvement in the weather and la increases in water temperature. Every period of good growth followed an improvement in t weather, the best growth following the steepest rise in temperature, of from 18° to 23° in the l week of July, 1948, which was a week of extraordinarily prolonged sunshine following four we of bad weather. Good growth also occurred towards the end of July, 1947, when the temperat had risen from 17° to 22° in sixteen days, at the end of June, 1948, when two peaks of 19° w attained ten and twenty days respectively after a temperature of 13·5°, and in the Roach dur June, 1949, when the temperature rose from 15° to 20° in twenty days, because of prolon sunshine and in spite of low air temperatures. The spatfall of late 1949, in the Crouch, see no exception to the rule. Water temperatures fell early in August because of strong, cold win

hen rose when the weather became warm, calm and dull. The bright sunshine which occurred owards the end of the month (Fig. 3) was followed by the spatfall. Growth of oyster larvae was ecorded every time the water temperature had increased by about 5° in two weeks. Occasionally t followed smaller increases, provided these were accompanied by prolonged sunshine. The ontinuously high water temperatures of 1949 were not very favourable to growth of oyster larvae.

Records from the Oosterschelde by Korringa (1941) show similar correlations. In 1938 an ncrease in water temperature of from 18° to 23° in ten days was followed by the best spatfall vhich he recorded: in 1936 a rise of from 16° to 22° in six days was followed by the main spatfall f the year.

This response to improved weather conditions is to be expected from populations of larvae vhich are limited in growth and numbers by food supply and the attacks of predators. It seems ikely that nannoplankton flagellates, at their usual concentrations of less than 5 per $mm.^3$, are omewhat too sparse for good growth of oyster larvae, and that they are generally kept at this evel by the grazing of more efficient feeders. Improved weather leads to more rapid multiplication f nannoplankton organisms, but as their population density increases their rate of removal by razing automatically increases too. There follows no very striking increase in the nannoplankton, ut much better growth of zooplankton, especially of those species which had previously been ear starvation level. If oyster larvae are abundant a good spatfall follows, but rapid growth of lankton animals and multiplication of such forms as ciliates and rotifers, together with high ates of survival amongst the planktotrophic larvae which are constantly being liberated by umerous benthic invertebrates, all make increased demands upon the nannoplankton, which is oon grazed back to the basic level, so that growth of those animals which are less efficient feeders s retarded again, even though the fine weather continues. Finally, the increase in zooplankton ncourages the development of those predators which appear in ephemeral swarms.

Bad weather, as in July 1948, seemed to retard the development even of the overwhelmingly uccessful larvae of *Elminius* (p. 31), and it is unlikely that this was due to low temperatures alone, or *Elminius* larvae can grow at much lower temperatures. Some setting of *Elminius* occurred uring the winter, when the weather was mild. Food supply must often be an important factor imiting the growth and numbers of animals which are produced as abundantly and which grow s rapidly as planktotrophic larvae and their competitors amongst the permanent plankton. The manner in which the proportion of benthic invertebrates with a planktotrophic larval stage falls ff in colder latitudes (Thorson, 1950) seems evidence of this.

It may be possible to promote growth of oyster larvae artificially to some extent. The weather annot be controlled, but increased nannoplankton production may follow addition of nutrient alts even during dull weather (Gaarder and Spärck, 1931). Such additions should be made autiously, for plant populations which are too dense may release metabolites harmful to oyster arvae (Korringa, 1951). The plans by the late Dr. Fabius Gross for fertilisation experiments in Loch Craiglin included trials with oysters, but the pH in that shallow, enclosed body of water, vith its abundant attached plants, reached levels far too high for the survival of oyster larvae (Orr, 1947). The later experiments in Kyle Scotnish, which is deeper and open to the sea through narrow channel, did not deal with oysters and the published accounts do not include pH records, ut Dr. D. T. Gauld kindly informs me that records of pH were taken and that these never xceeded 8·4. This is within the limits tolerated by oyster larvae (Cole, 1936; 1939). There were narked increases in abundance of the benthos in Kyle Scotnish (Raymont, 1950), including lam-llibranchs, such as *Montacuta bidentata* and *Abra prismatica*, the larvae of which, like oyster arvae, are planktotrophic. Competitors of oysters would inevitably benefit from effective fertili-ations of Essex creeks, but many of these, such as *Elminius*, are short-lived and produce swarms f larvae which would help to feed adult oysters (Savage, 1925), whilst *Crepidula* grows slowly and ould be kept down by dredging, if there were enough oysters to make more intensive dredging rofitable.

SUMMARY

The oyster-producing creeks near Burnham are long channels swept by tidal currents of full alinity seawater, which cause turbidity but do not sweep many larvae out to sea. The shallow vaters, being of similar temperature to the air, become very warm in fine summer weather. There re few fixed plants, for stable substrata are scarce; the maximum pH observed was 8·2.

Nannoplankton organisms greater than 1μ in size varied between 1 and 50 per mm.^{3} The flagellat which are important as food for oyster larvae were usually about 5 or 10 per mm^3. during fi weather, when growth of oyster larvae took place, but were scarcer during bad weather.

Liberations of larvae and their growth or disappearance were recorded by routine 100 plankton samples, pumped from several stations in the Roach and Crouch. Most of the pea of abundance of newly-liberated larvae occurred at neap tides, which indicates that spawni took place mainly at spring tides, since the incubation period is about a week. Few larvae we liberated at low slack water. The sizes of larvae at liberation and probably at metamorpho were slightly smaller in the second half of the season than in the first half. When the wat temperature in the upper reaches was higher than in the lower reaches, larvae from the upp reaches became ready for metamorphosis at a smaller average size than those from the low reaches. The planktonic stage lasted less than a week at 22°–23°, more than 11 days at 17°–18 From 5 per cent to 8 per cent of the larvae produced in a season survived to metamorphosis, b great short-term fluctuations in survival rate occurred: usually it was negligible, once it was ov 30 per cent. Breeding stocks were concentrated near Paglesham and concentrations of larv were much greater in the Roach than in the Crouch, but many larvae were carried down into t Crouch at low water. Tidal currents were strong enough to carry larvae 5 miles in 6 hrs., so larv generally became widely distributed by the time they reached setting size.

Spatfall peaks were recorded by exposing slates for weekly periods at several stations. Th spatfall on naturally occurring surfaces was also studied. It was much heavier on shells fro grounds which had been densely stocked with oysters, than from neighbouring grounds whi had been left unstocked, probably because setting oyster larvae are gregarious. Slates on m grounds were soon smothered by the recently imported barnacle *Elminius modestus*, which increas in abundance in successive years. Surfaces became crowded with it at remarkably even densit of from 10 to 90 per sq. cm. and were then unfavourable for the attachment of oyster larv Setting of other sessile organisms was comparatively light: several species were found p ponderantly on either the upper or the lower surfaces of the horizontal slates. Many small oys spat were smothered by rapidly spreading colonies of *Membranipora lacroixii*.

Shells in bags, limed tiles and concrete-coated egg-box partitions were given trials as collect of spat in various localities. No advantage was gained by placing them near oyster stocks; inde siting on bare mud is to be preferred, for there setting of barnacles is less intense. Smother with *Elminius modestus* was a serious problem and further trials are needed before using artific collectors on a commercial scale.

The death-rate amongst spat was very high soon after setting, but gradually became low Abundant production of young oysters in the upper reaches of Essex creeks was related to presence there of wide areas of shelly bottom and the absence of some animals which dest recently settled spat.

Although the 1947 season was warm the yield of oyster larvae and spat was very low, breeding stocks were sparse and in poor condition after the previous severe winter. The 1 season was generally cold and rough, but the last week of July was very sunny and warm, a oyster larvae then showed a high rate of growth and survival, producing an intensive, short-li spatfall. The 1949 season was warm and dry. Larvae were numerous but their rates of gro and survival were only moderate. Throughout the three years good growth of oyster lar occurred only after periods of marked improvement in the weather and large increases in wa temperature. Continued good weather and sustained high temperature were less favoura Probably oyster larvae and their competitors were usually limited in growth and numbers by f supply and perhaps by the attacks of those predators which appear in ephemeral swarms. Cauti attempts should be made to increase the food supply by the use of fertilisers.

ACKNOWLEDGMENTS

These investigations were planned and directed by Dr. H. A. Cole, from the Fishe Experiment Station, Conway. I am very grateful to him for his advice and for examining criticising this account.

I am particularly grateful to Mr. G. Duncan Waugh and Mr. J. P. Stevenson, who colle most of the data relating to abundance and growth of oyster larvae during 1948 and 1

spectively. I must also thank Mr. E. P. Bourne, for taking most of the plankton samples and r many discussions about oyster culture in Essex, and Mr. P. J. Warren, for most of the timations of salinity and pH.

It is a great pleasure to acknowledge the friendly co-operation of the Directors, foremen and edgermen of Messrs. Smith Brothers, Burnham-on-Crouch, and the Seasalter and Ham Oyster shery Company, Whitstable.

REFERENCES

TTLE, H. I., 1932. Rhythmic sexual maturity and spawning of certain bivalve molluscs. *Contr. Canadian Biol. and Fish.*, **7**, 257.

UCE, J. R., KNIGHT, MARGERY, and PARKE, MARY W., 1940. The rearing of oyster larvae on an algal diet. *J. Mar. Biol. Assn. U.K.*, **24**, 337.

TCHER, R. W., 1952. Contributions to our knowledge of the smaller marine algae. *J. Mar. Biol. Assn. U.K.*, **31**, 175.

RRIKER, M. R., 1951. Ecological observations on the distribution of the oyster larvae in New Jersey estuaries. *Ecol. Monogr.*, **21**, 19.

RRUTI, A., 1941. Osservazioni ed esperimenti sulle cause di distruzione delle larve d'ostrica nel Mar Piccolo e nel Mar Grande di Taranto. *Archivio di Oceanografia e Limnologia*, **19**, 165.

LE, H. A., 1936. Experiments in the breeding of oysters (*Ostrea edulis*) in tanks, with special reference to the food of the larva and spat. *Fish. Invest. Series II*, **15**, No. 4.

—, 1938*a*. The fate of the larval organs in the metamorphosis of *Ostrea edulis*. *J. Mar. Biol. Assn. U.K.*, **22**, 469.

—, 1938*b*. A system of oyster culture. *J. du Conseil*, **13**, 221.

—, 1939. Further experiments in the breeding of oysters in tanks. *Fish. Invest. Series II*, **16**, No. 4.

—, 1940. Effect of the severe winter of 1939–40 on British oyster-beds. *Nature*, **145**, 976.

—, 1941. The fecundity of *Ostrea edulis*. *J. Mar. Biol. Assn. U.K.*, **25**, 243.

—, 1942. The American whelk tingle, *Urosalpinx cinerea* (Say), on British oyster beds. *J. Mar. Biol. Assn. U.K.*, **25**, 477.

—, 1951. The British oyster industry and its problems. *Rapp. Cons. Explor. Mer.*, **128**, 7.

— and KNIGHT-JONES, E. W., 1939. Some observations and experiments on the setting behaviour of larvae of *Ostrea edulis*. *J. du Conseil*, **14**, 86.

—, ——, 1948. The setting behaviour of larvae of the European flat oyster, *Ostrea edulis L.*, and its influence on methods of cultivation and spat collection. *Fish. Invest. Series II*, **17**, No. 3.

—, ——, 1949. Quantitative estimation of marine nannoplankton. *Nature*, **164**, 694.

SP, D. J., and CHIPPERFIELD, P. N. J., 1948. Occurrences of *Elminius modestus* (Darwin) in British waters. *Nature*, **161**, 64.

LIDO, P., 1948. L'huître du Morbihan. Paris.

DGSON, R. W., 1922. *Noctiluca* as an enemy of the oyster. *Nature*, **110**, 343.

DMANN, W., 1934. Untersuchungen über die Lebensgeschichte der Auster. No. 5. Uber die Entwicklung und die Anatomie der " ansatzreifen ". Larve von *Ostrea edulis* mit Bemerkungen über die Lebensgeschichte der Auster. *Wiss. Meeresuntersuch. Abt. Helgoland*, **19**, No. 6.

ARDER, T., and SPÄRCK, R. 1931. Biochemical and biological investigations of the variations in the productivity of the West Norwegian oyster pools. *Rapp. Cons. Explor. Mer.*, **75**, 47.

LTSOFF, P. S., 1930. The role of chemical stimulation in the spawning reactions of *Ostrea virginica* and *O. gigas*. *Proc. Nat. Acad. Sci., Washington*, **16**, 555.

—, 1932. Spawning reactions of three species of oysters. *J. Wash. Acad. Science*, **22**, 65.

RBARINI, P., 1936. Rhythmes de croissance des oocytes et d'incubation des larves chez *Spirorbis borealis* Daudin. *C.R. Soc. Biol., Paris*, **122**, 157.

MPEL, M., 1938. Recherches sur la consommation d'oxygène de quelques animaux aquatiques littoraux. Rythme des oxydations et rythme des marées. *Ann. de Physiol.*, **14**, 914.

VINGA, B., 1939. Prediction of the time of setting of oyster spat and a method of control. *J. du Conseil*, **14**, 394.

MAN, A. 1938. Rapport sur la reproduction des huîtres indigènes dans le Morbihan et le Finistere. *Rev. Trav. Pêches Marit.*, **11**, 189.

K, P. P. C., HORST, R., KERBERT, C., VAN REES, J., SCHEPMAN, M. M. and VIGELIUS, W. J., 1884. Bijdragen tot de kennis der Oosterschelde fauna. *Tijdschr. Ned. Dierk. Ver. Suppl. Deel* 1.

, T., HATANAKA, M., SATO, R., and SAKAI, S. 1951. Ecology of Mangoku-Ura inlet with special reference to the seed-oyster production. *Sci. Rep. Res. Inst. Tohoku Univ.* D 1–2, 137.

, T. and SATO, R., 1949. Culture of water fleas, *Moina macrocopa* Straus, on non-coloured naked flagellates diet. *Bull. of the Inst. of Agric. Res., Tohoku Univ.*, **1**, 44.

GENSEN, C. C. BARKER, 1943. On the water transport through the gills of bivalves. *Acta physiol. Scand.*, **5**, 297.

TEVEN, G. L., 1941. The biology and cultivation of oysters in Australia, I, Some economic aspects. *C.S.I.R. Australia, Div. of Fish., Rep. No.* 5.

GHT-JONES, E. W., 1948. *Elminius modestus:* another imported pest of east coast oyster beds. *Nature*, **161**, 201.

, 1951*a*. Aspects of the setting behaviour of larvae of *Ostrea edulis* on Essex oyster beds. *Rapp. Cons. Explor. Mer.*, **128**, 30.

KNIGHT-JONES, E. W., 1951*b*. Preliminary studies of nannoplankton and ultraplankton systematics abundance by a quantitative culture method. *J. du Conseil*, **17**, 140.
——, 1951*c*. Gregariousness and some other aspects of the setting behaviour of *Spirorbis*. *J. Mar. Assn. U.K.*, **30**, 201.
——, and STEPHENSON, J. P., 1950. Gregariousness during settlement in the barnacle *Elminius mode* Darwin. *J. Mar. Biol. Assn. U.K.*, **29**, 281.
——, and WALNE, P. R., 1951. On *Chromulina pusilla* Butcher, a dominant member of the ultraplankt *Nature*, **167**, 445.
KORRINGA, P., 1941. Experiments and observations on swarming, pelagic life and setting in the Europ flat oyster, *Ostrea edulis* L. *Arch. Néerland. Zool.*, **5**, 1.
——, 1947. Relations between the moon and periodicity in the breeding of marine animals. *Ecol. Mon* **17**, 347.
——, 1950. A review of the papers on molluscs presented at the special scientific meeting on she of the International Council for the Exploration of the Sea, Edinburgh. 1949. *J. du Conseil*, **17**
——, 1951. Difficulties encountered in tank-breeding of oysters (*Ostrea edulis*). *Rapp. Cons. Explor. M* **128**, 35.
LADOUCE, R., 1938. Observations sur la production du naissain dans le bassin d'Arcachon en 1938. *Trav. Pêches Marit.*, **11**, 207.
LAVER, H., 1916. The Colchester Oyster Fishery. Colchester.
LOOSANOFF, V. L., 1950. Variations in Long Island Sound oyster set. *Atlantic Fisherman*, **30**, 15.
——, MILLER, W. S., and SMITH, P. B., 1951. Growth and setting of larvae of *Venus mercenaria* in rela to temperature. *J. Mar. Res.*, **10**, 59.
——, NOMEJKO, C. A., 1951. Spawning and settling of the American oyster, *O. virginica*, in relatio lunar phases. *Ecology*, **32**, 113.
MISTAKIDIS, M. N., 1952. Quantitative studies of the bottom fauna of Essex oyster grounds. *Fish. In Series II*, **17**, No. 6.
NEEDLER, A. W. H., 1941. Oyster farming in Eastern Canada. *Fish. Res. Bd. Canada*, **60**, 1.
NELSON, T. C., 1928. Relation of spawning of the oyster to temperature. *Ecology*, **9**, 145.
NORRIS, E., JONES, L. W. G., LOVEGROVE, T., and CRISP, D. J., 1951. Variability in larval stage cirripedes. *Nature*, **167**, 444.
ORR, A. P., 1947. An experiment in marine fish cultivation: II. Some physical and chemical condi in a fertilised sea-loch. *Proc. Roy. Soc. Edin.*, B. **63**, 3.
ORTON, J. H., 1924. An account of investigations into the cause or causes of the unusual mortality ar oysters in English oyster beds during 1920 and 1921. *Fish. Invest. Series* II, **6**, No. 3.
——, 1926. On lunar periodicity in spawning of normally grown Falmouth oysters in 1925 with compa of spawning capacity of normally grown and dumpy oysters. *J. Mar. Biol. Assn. U.K.*, **14**, 1
——, 1927. On incomplete spawning and the problem of fertilisation in *Ostrea edulis*. *Nature*, **120**,
——, 1936. Observations and experiments on sex-change in the European oyster (*Ostrea edulis*). Pa A simultaneous study of spawning in 1927 in two distinct geographical localities. *Mém. Mus. Hist. Nat. Belg. Ser.* 2, **3**, 997.
——, 1937. Oyster Biology and Oyster-culture. London.
OSBURN, R. C., 1944. A survey of the Bryozoa of Chesapeake Bay. *Chesapeake Biol. Lab., Publ.*
PARKE, MARY W., 1949. Studies on marine flagellates. *J. Mar. Biol. Assn. U.K.*, **28**, 255.
PRYTHERCH, H. F., 1929. Investigation of the physical conditions controlling spawning of oysters an occurrence, distribution and setting of the oyster larvae in Milford Harbor, Connecticut. *U.S. Bur. Fish.*, **44**, 429.
RANSON, G., 1938. Contribution à l'êtude du développement de l'huitre Portugaise, *Gryphaea ang* Lmk. *Bull. Mus. Nat. d'Hist. Nat. Paris.* 2*e Série*, **10**, 410.
RAYMONT, J. E. G., 1950. A fish cultivation experiment in an arm of a sea-loch. IV. The bottom f of Kyle Scotnish. *Proc. Roy. Soc. Edin., B.*, **64**, 65.
SAVAGE, R. E., 1925. The food of the oyster. *Fish. Invest. Series II*, **8**, No. 1.
SPÄRCK, R., 1929. Studies on the biology of the oyster. VI. Some observations on the spawni *Ostrea edulis* in the Limfjord with special reference to the problem of lunar periodicity. *Danish Biol. Stat.*, **35**, 101.
THORSON, G., 1950. Reproductive and larval ecology of marine bottom invertebrates. *Biol.* **25**, 1.
WELLS, A. L., 1938. Some notes on the plankton of the Thames Estuary. *J. Animal Ecol.*, **7**, 105.

(15471) Wt. 2053—3238 K5 8/52 D.L.

Crown Copyright Reserved

PRINTED AND PUBLISHED BY HER MAJESTY'S STATIONERY OFFICE

To be purchased from

York House, Kingsway, LONDON, W.C.2 423 Oxford Street, LONDON, W.1
P.O. Box 569, LONDON, S.E.1
13a Castle Street, EDINBURGH, 2 1 St. Andrew's Crescent, CARDIFF
39 King Street, MANCHESTER, 2 Tower Lane, BRISTOL, 1
2 Edmund Street, BIRMINGHAM, 3 80 Chichester Street, BELFAST
or from any Bookseller

1952

Price 3*s.* 6*d.* net

PRINTED IN GREAT BRITAIN

S.O. Code No. 24-52-18-2